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A Study of the Birds of the Big Basin Region of California

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Introduction

Within recent years many regional studies have been made on the occurrence, distribution and habits of vertebrates within limited areas. These works have proven invaluable, not only in theory to the student of natural history but also in a very practical sense in aiding in the administration of certain of our national and state recreational areas and wildlife sanctuaries. One of the most important services that the field biologist can contribute is to accurately record, for the use of present and future generations, the ecological relationships of plants and animals within certain definitely circumscribed regions. This is especially desirable in those areas where civilization is rapidly encroaching upon and changing the native wildlife complex. It is here probably, rather than in remote wilderness regions, that we should devote most of our energy in accumulating factual material. This should not be confined merely to casual observation, but rather to the active recording of all information pertaining to the welfare and existence of native species. With such factual information once available we are in a better position to judge the relative worth of various areas from a biological viewpoint and may, through cooperative efforts, bring about more adequate and complete preserves for our native wildlife.

The primary purpose of this study has been to present an account of the occurrence, distribution and, in so far as possible, ecological relationships of those avian species, as found at present, in the Big Basin Region of the Santa Cruz Mountains of California, including California Redwood State Park, San Mateo County Memorial Park and a large portion of privately owned land between and to the west of these public holdings. The parks afford permanent refuge to those native species that occur within their confines. Unfortunately, however, practically none of the coastal land situated to the westward is publicly owned. This area, though largely under private ownership and rapidly being devoted to economic interests, has been included for several reasons. It ties in naturally with the more interiorly state- and county-owned properties, thus combining to form a complete cross-section of the western slope of this portion of the Santa Cruz Mountains from their crest to the Pacific Ocean. It is steadily undergoing a change from its original condition, as a result of human usage. Each year, consequently, it becomes more difficult to visualize this

region as it existed primitively. Furthermore, it is possible and to be hoped that at least a part of this coastal region may ultimately be acquired as a wildlife sanctuary, protecting examples of the strictly coastal biota in the manner this is now accomplished in the adjoining mountainous California Redwood State Park and San Mateo County Memorial Park.

The author wishes to thank the United States National Park Service and the California Academy of Sciences for many assistances received, as it was under the auspices of both these organizations that this work was carried on.

Methods

Field work carried on in this study has consisted in observation rather than the securing of specimens. The subspecific determination of forms occurring within the confines of the area involved has not been included as within the scope of this report. Such collecting as was done, as a rule, was incidental except in the case of shore birds, in which instance effort was made to obtain specimens for stomach content analyses.

A total of 176 days were spent in the field, between May 21, 1935, and March 15, 1939. These were not all primarily devoted to ornithological observations but at least a portion of each day was so spent. Observations made on one day (July 22, 1933) prior to the period of this study are included because of certain pertinent information then obtained. The following tabulation shows the number of days spent in the field during each month of the year:

January	1	July	22
February	18	August	4
March	34	September	2
April	33	October	3
May	28	November	1
June	30	December	1

As is evidenced by this tabulation most of the field work was carried on between late winter and late summer. Fall and early winter field days were devoted mainly to observations on shore birds and waterfowl.

The information contained in the following pages refers only to those species actually observed by the writer. No attempt has been made to include published records, earlier accounts, or to list specimens taken prior to this undertaking. Where the slightest doubt existed as to the correct identity of species observed in the field such records were discarded. It may, likewise, be stated that no special effort was made to obtain more information on rarer forms than their relative abundance would seem to justify. It was thought that the greatest value could be derived by devoting most of the time to study of the more common species, those that constitute the great bulk of the avian population and, consequently, are probably of greatest importance in a biotic community.

Species accounts are arranged in accordance with the A.O.U. checklist of 1931.

Geographic and Zonal Position

The Big Basin Region, as here defined, is situated along the coastal portion of central California, approximately two-thirds of the way south between San Francisco and Monterey bays. The most northerly part is about thirty-five miles south of the Golden Gate in a straight line and the southernmost portion is fifteen miles north of the town of Santa Cruz. Based upon the United States Geological Survey map, Santa Cruz Quadrangle, the area studied was limited on the north by a line run due east eight miles, from the sea coast one mile north of the mouth of Pescadero Creek, to Jones Gulch. The eastern boundary extends south from Jones Gulch to the Butano Ridge, along the crest of this ridge and its continuation China Grade, thence south to Eagle Rock at the north end of Ben Lomond Mountain. The southern boundary is limited on the east by Eagle Rock and on the west by a point one-half mile south of Greyhound Rock on the Pacific Ocean.

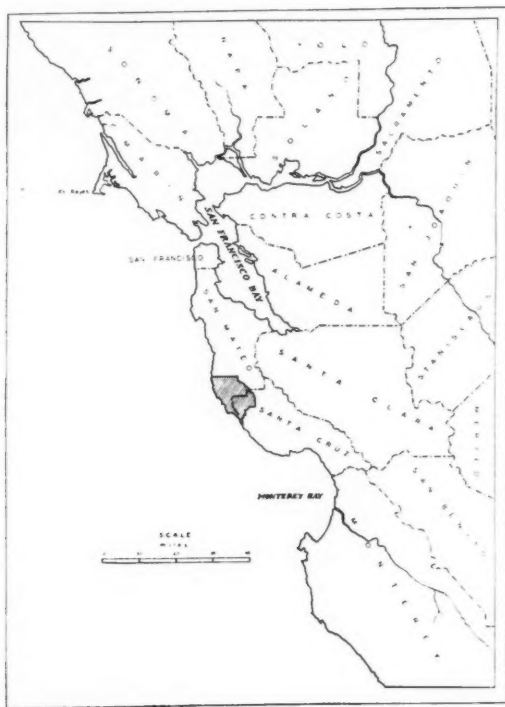


Fig. 1.—Map of west-central California showing the geographic position of the Big Basin region, as here defined.

This area includes about one hundred and eight square miles of territory with twenty-one miles of shore line. The most inland point is on Butano Ridge, where it is some nine miles to the sea. All of the drainages within the region flow to the west and southwest. The largest of these hydrographic basins is the Pescadero, which in its entirety occupies sixty square miles. Only the lower portion of this was included within the northern part of the area. The next largest hydrographic basin is the Waddell, whose southern limits roughly demark the southern boundary of the area. The only additional drainages of any size occurring between the Pescadero-Butano and Waddell are the Gazos and Whitehouse, each of which is relatively small. The eastern boundary of the region is marked by a series of connected ridges that separate these western- and southwestern-flowing drainages from the rather extensive southeasterly-flowing San Lorenzo-Boulder Creek hydrographic basin. The latter is the largest in the Santa Cruz Mountains and includes about one hundred and twenty-six square miles.

The Big Basin Region, generally speaking, is near the southern border of the humid coast belt and within the Transition Life Zone. The area, particularly the eastern portion, is subject to a great deal of precipitation during the winter months. While no data are available regarding annual rainfall in the Big Basin proper, weather records compiled by the Weather Bureau of the United States Department of Agriculture for Boulder Creek, between 1888

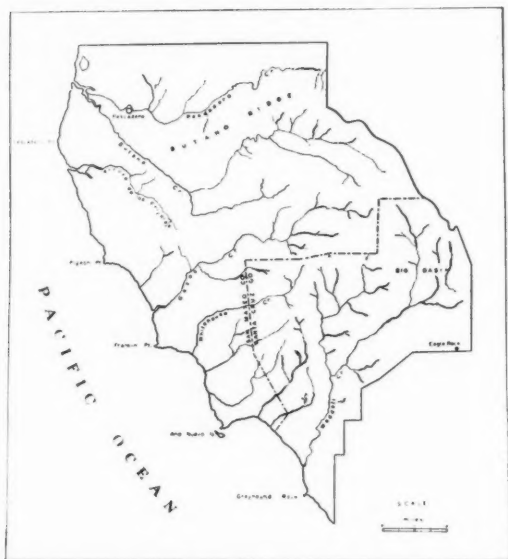


Fig. 2.—Map of the Big Basin region in which observations were carried on.

and 1916, show the average annual rainfall to be 55.57 inches. Boulder Creek, five miles southeast of the boundary of California Redwood State Park, is on the eastern side of the mountains, within the San-Lorenzo-Boulder Creek watershed, and, according to those residents familiar with the region, receives less rain than does the Big Basin. Along the coastal portion the rainfall is of course much less. During the summer months, when the rainfall is negligible, heavy fogs regularly roll in from the ocean and remain during the night and early morning, thus tending to increase the humidity during the warmest and driest time of the year. Along the lower coastal parts these fogs often remain all day and, not infrequently, many consecutive days will pass without the sun being visible.

Although the area as a whole may be considered as within the Transition Life Zone there are many so-called "islands" of Upper Sonoran that occur scattered about. Most of the ridges in the western section are of sandstone formation near the surface and are covered with a loose diatomaceous shale. This shale is nearly white in color and may be seen a number of miles away in places, especially as it is only sparsely covered with a hard type of chaparral. It reflects much light and radiates considerable heat so that the temperature on these ridges may become very high in the middle of the day, particularly on the south-facing slopes. Many extensive outcroppings of sandstone, locally, produce the same results.

Major Associations

For the sake of convenience in discussion and also because various biological communities in any moderately extensive area, even though largely dependent upon one another, may be roughly segregated into broad categories, the use of the term association is here employed. Each so-called association may in turn be subdivided into various habitats almost indefinitely but this has been reserved for species accounts, where sufficient information has been available. Eight major associations are listed as follows:

Redwood-Douglas fir	Grassland
Woodland	Riparian
Hard chaparral and knob-cone pine	Marsh
Coastal chaparral	Shore

Redwood-Douglas fir.—Much of the esthetic charm and at least potential commercial value of the mountainous portions of the region studied lies in its splendid forests of coast redwood. These stands, while not as spectacular or extensive as those found in the northwestern part of the state, do excel in central California. They, likewise, represent the southernmost extensive forest of large redwoods in existence. To these stately giants undoubtedly all other associated forms of plant and animal life now owe their present security and future preservation. Their presence was entirely the motive for creating the parks now existing in this region and in which conservation is one of the basic and primary functions.

Pure stands of redwood do not occur in the Santa Cruz Mountains. In fact throughout the entire range of the coast redwood, which occupies some

eighteen hundred and fifty square miles in coastal California and extreme southern Oregon, pure stands occupy less than fifty square miles according to Sudworth (*Forest Trees of the Pacific Slope*, 1908, p. 147). In a certain sense, with all due respect to the solemn grandeur and beauty of such forests, it might be said this is decidedly advantageous to bird life as a whole. Solid areas of redwood are generally rather unproductive from an ornithological point of view. The most apparent reason for this would seem to lie in the



Fig. 3.—Redwood-Douglas fir forest bordering a small clearing known as Potrero Meadow in the Big Basin, Santa Cruz County, California. Photograph taken April 10, 1936.



Fig. 4.—Sky Meadow in the Big Basin, Santa Cruz County, California, showing an oak-madrone woodland in the background with a redwood-Douglas fir forest still farther back. Photograph taken April 10, 1936.

scarcity of suitable and available food materials. Plants producing copious quantities of seeds, such as composite species, are of very limited occurrence. Insect populations are also relatively low. In fact redwood trees themselves are notably free from insect attack. It may be said, in general, that mixed types of forests invariably contain more species of birds than do pure stands.

The following is a list of plants which, while not all typical of the redwood-Douglas fir forest, were found frequently in the association in the areas studied:

Gymnogramme triangularis. Gold fern
Polypodium vulgare. Licorice fern
Pteris aquilina. Bracken
Lomaria spicant. Deer fern
Woodwardia radicans. Chain fern
Athyrium filix-foemina. Lady fern
Polystichum munitum. Sword fern
Aspidium rigidum var. *argutum*.

California wood fern
Pseudotsuga taxifolia. Douglas fir
Sequoia sempervirens. Redwood
Torreya californica. California nutmeg
Disporum hookeri. Fairy bells
Smilacina sessilifolia. Slim solomon
Smilacina amplexicaulis. Fat solomon
Clintonia andrewsiana. Clintonia
Scoliopus bigelovii. Slink-pod
Trillium ovatum. Wake robin
Iris douglasiana. Mountain iris
Corylus rostrata. California hazel
Lithocarpus densiflora. Tan oak
Myrica californica. Wax myrtle

Aquilegia truncata. Columbine
Vancouveria parviflora. Inside-out flower
Dentaria integrifolia. Milk-maids
Rubus parviflora. Thimble-berry
Rubus leucodermis. Western raspberry
Fragaria californica. Wood strawberry
Rosa gymnocarpa. Wood rose
Oxalis oregana. Redwood sorrel
Rhamnus purshiana. Cascara sagrada
Ceanothus thyrsiflorus. California lilac
Ceanothus papillosus. Ceanothus
Viola sargentosa. Wood violet
Viola glabella. Violet
Viola ocellata. Western heart's ease
Pterospora andromeda. Pine drops
Gaultheria shallon. Salal
Arbutus menziesii. Madrone
Vaccinium ovatum. Huckleberry
Vaccinium parvifolium. Red-bilberry
Trientalis europea var. *latifolia*.
 Star flower
Micromeria chamissonis. Yerba buena

The actual composition of the forest varies to a considerable extent, depending upon certain physical features in the environment such as slope exposure and drainage. On low flats and in canyon bottoms the redwood dominates the Douglas fir, whereas higher up on many slopes and even on the tops of certain ridges Douglas fir is dominant, sometimes completely replacing the redwood. These floral differences within the same general association were found to directly affect the local distribution of a number of species of birds. To cite certain examples, Stellar jays, chestnut-backed chickadees and juncos were uniformly distributed throughout. Band-tailed pigeons, on the other hand, were noted mostly on slopes where Douglas fir was dominant. This, likewise, was true of hairy woodpeckers and red-breasted nut-hatches. The presence of California woodpeckers seemed largely dependent upon the occurrence of oaks in numbers. Brown creepers were somewhat more numerous where redwoods were dominant. Winter wrens were noted only in the darkest and dampest canyons where the redwoods grew almost to the exclusion of Douglas fir.

Logged areas present a somewhat different aspect, especially where the second growth has not as yet attained to an advanced stage. Small Douglas firs and low stump-sprouted redwoods combined with woodland and chaparral species, such as naturally occur in logged areas in the normal course of plant

succession, frequently result in biological islands of a lower zone. Typically woodland and chaparral species are rapidly attracted to such localities.

Woodland.—This association occurs normally in this region as a fringe bordering more extensive coniferous forests and usually occupies an intermediate position between the latter and the also more extensive chaparral tracts. The arborescent vegetation is composed principally of non-coniferous trees, such as madrone, tan oak, coast live oak, canyon live oak and California laurel. Numerous shrubs and herbs grow beneath the partial protection afforded by these trees. The following floral list indicates the plants found most commonly in this association:

Pteris aquilina. Bracken
Athyrium filix-foemina. Lady fern
Zygadenus fremontii. Star zygadene
Brodiaea capitata. Blue dicks
Calochortus albus. White globe lily
Fritillaria lanceolata. Checker lily
Smilacina sessilifolia. Slim solomon
Smilacina amplexicaulis. Fat solomon
Trillium ovatum. Wake robin
Iris douglasiana. Mountain iris
Habenaria elegans. Rein-orchis
Quercus chrysolepis. Canyon live oak
Quercus agrifolia. Coast live oak
Quercus wislizenii. Interior live oak
Lithocarpus densiflora. Tan oak
Aquilegia truncata. Columbine
Delphinium nudicaule. Red larkspur
Umbellaria californica. California laurel
Dentaria integrifolia. Milk-maids
Holodiscus discolor. Cream bush

Rubus leucodermis. Western raspberry
Fragaria californica. Wood strawberry
Lathyrus californicus. Pea
Polygala californica. Milkwort
Rhus diversiloba. Poison oak
Aesculus californica. Buckeye
Ceanothus papillosus. Ceanothus
Ceanothus thyrsiflorus. California lilac
Pterospora andromeda. Pine drops
Arbutus menziesii. Madrone
Convolvulus luteolus. Morning-glory
Nemophila sepulta. Nemophila
Salvia mellifera. Black sage
Sphacele calycina. Pitcher sage
Solanum umbelliferum. Blue witch
Scrophularia californica. Figwort
Symphoricarpos albus. Snow berry
Lonicera hispidula var. *californica*. California honeysuckle
Lonicera involucrata. Honeysuckle
Stachys californica. Hedge nettle

This woodland type proved to be the most productive association of all those studied as regards avifauna. Although there were probably less than a dozen species of birds which were restricted solely to woodlands there were a large number of forms typical of the redwood-Douglas fir forest and chaparral which were found almost equally plentiful in woodlands. Several factors seemingly contributed to this productivity. A great diversity of plant life was present which was correlated with a large insect population, at least of a certain type. Judging purely from observations made in the field the author came to the opinion that winged insects were more numerous in the woodlands than either in the densely forested areas or out in the hot, dry chaparral during the spring and summer months. This observation was substantiated by the proportionately large number of insectivorous birds present, flycatchers, vireos, and warblers predominating. Furthermore, there was an abundance of plant cover, both in the form of trees and underbrush, thus providing a number of habitats. Such species as spotted towhees, Bewick wrens and ash-throated flycatchers which were regular chaparral inhabitants were equally abundant in suitable portions of woodlands. Likewise, chestnut-backed chickadees, Oregon juncos and hermit thrushes were frequently found in woodlands as well as in dense conifer tracts.

Hard chaparral and knob-cone pine.—There occurs over a good deal of this area a "hard" type of chaparral, as defined by Jepson (A Manual of the Flowering Plants of California, 1925, p. 6), composed of a number of more or less xerophytic types of shrubs. Dominant among these are various species of manzanita, chamise, buck-brush and chaparral pea. This association was largely limited to the south- and west-facing slopes of the higher ridges, mostly above the redwood belt, altitudinally. It is particularly characteristic of the so-called "Chalks" in the southwestern portion of this region where the higher ridges are covered with white diatomaceous shale. Herbaceous growth is extremely sparse. Knob-cone pines occur scatteringly and locally throughout, rarely being present in numbers sufficient to form a forest type of cover. They are found most abundantly on Pine Mountain and on the southwestern slope of the China Grade. The following list of plants are those species noted to occur more or less commonly in this association:

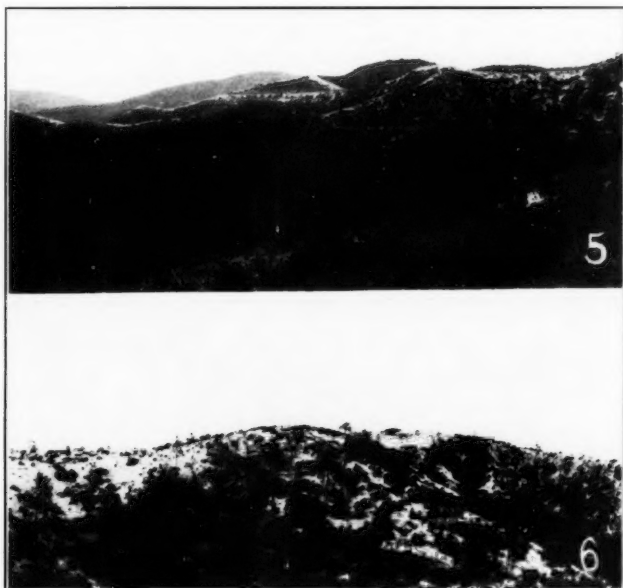


Fig. 5.—Hard chaparral on the ridges with redwood and Douglas fir growing in the canyon, near the head of the East Fork of Berry Creek, a tributary to the East Fork of Waddell Creek, Santa Cruz County, California. Photograph taken April 16, 1936.

Fig. 6.—Hard chaparral and knob-cone pine growing along "The Chalks", Santa Cruz County, California. Photograph taken April 16, 1936.

Pinus attenuata. Knob-cone pine
Quercus dumosa. Scrub oak
Quercus chrysolepis.
 Canyon live oak (scrub var.)
Quercus agrifolia.
 Coast live oak (scrub var.)
Castanopsis chrysophylla.
 Giant chinquapin
Dendromecon rigida. Bush poppy
Adenostoma fasciculatum. Chamise
Photinia arbutifolia. Toyon
Pickeringia montana. Chaparral pea
Lotus scoparius. Deer weed
Rhamnus californica. Coffee berry

Ceanothus cuneatus. Buck-brush
Helianthemum scoparium. Bush-rose
Lomatium dasycarpum. Hog-fennel
Arctostaphylos crustacea. Manzanita
Arctostaphylos sensitivus. Manzanita
Eriodictyon californicum. Yerba santa
Antirrhinum vagans. Snapdragon
Diplacus aurantiacus. Bush monkey-flower
Castilleja foliolosa. Woolly painted cup
Pedicularis densiflora. Indian warrior

The number of species of birds was found to be somewhat less here than in the coastal chaparral. This might be attributed, in part, to the relative scarcity of plants producing seeds in large quantities; also to the scarcity of small, open, grassy clearings intermingled with the brush. The presence of knob-cone pines proved attractive to certain birds such as pigmy nuthatches, California purple finches and Mexican bluebirds, providing both perches and, to some extent, food. A number of species that, strictly speaking, were not inhabitants of this association spent considerable time foraging over these chaparral-covered ridges. Among these may be mentioned turkey vultures, red-tailed hawks and purple martins.

Coastal chaparral.—Coastal brush land occurs as a strip of varying width and irregular occurrence along the western margin of this area. In the north-western portion it extends quite a ways inland, locally, sometimes as much as

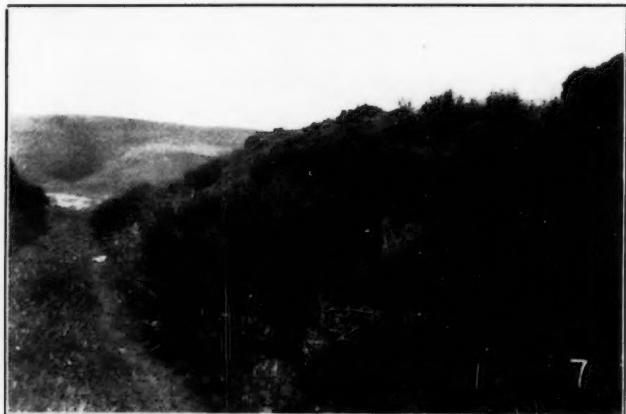


Fig. 7.—Coastal brush, composed principally of lupine and lizard-tail, near the mouth of Pescadero Creek, San Mateo County, California. Photograph taken March 2, 1938.

five miles. In the southwestern portion it is extremely narrow, in places being not more than several hundred yards in width, and is replaced to the east either by forested land or hard chaparral. Furthermore, human usage has increased its diminution in many places. Here, as elsewhere along the coast, it has been the custom of land owners for years past to burn brush in the early winter to increase grazing land for domestic stock.

The following species of plants were found to be of most importance in the formation of a coastal type of brush cover:

<i>Eriogonum latifolium</i> . Buckwheat	<i>Conium maculatum</i> . Poison hemlock
<i>Rubus vitifolius</i> . Blackberry	<i>Solanum nigrum</i> . Black nightshade
<i>Lupinus arboreus</i> . Bush lupine	<i>Erigeron glaucus</i> . Seaside daisy
<i>Rhus diversiloba</i> . Poison oak	<i>Baccharis pilularis</i> . Chaparral broom
<i>Rhamnus californica</i> . Coffee berry	<i>Eriophyllum staechadifolium</i> . Lizard-tail
<i>Echinocystis fabacea</i> . Common man-root	<i>Artemisia californica</i> . California sagebrush

In character this coastal chaparral differs very appreciably from the so-called hard chaparral occurring on the ridges situated farther inland. With few exceptions the species of plants forming these two chaparral types are entirely different. Whereas the hard chaparral is composed of wiry, but well-spaced, semi-xerophytic types of shrubs that are readily penetrated by sunlight, the coastal chaparral consists of dense, close-growing species of considerably greater water requirement.

A certain number of species of birds were common to both associations, but quite a few others such as white-crowned sparrows, golden-crowned sparrows and willow goldfinches, while common in the coastal chaparral, were not observed inland.

Grassland.—Probably no other single association has been more altered from its original state at the hands of man than the grassland as it must once have existed along the coastal plain and in the lower portions of some of the broader valleys. Human settlement in inhabitable country is usually



Fig. 8.—Open meadow land with chaparral and forest in the background, Hidden Valley, San Mateo County, California. Photograph taken March 15, 1939.

influenced by the presence of such land. It is generally the most readily productive, hence the first to be subjected to modification and change. This is no less true in the region studied than elsewhere in the world at large. The production of truck crops, such as artichokes, Brussels sprouts, peas, beans and lettuce, has resulted in cultivation of much of the open land. Most of the remainder has been used for stock grazing for many years. In the former areas no native vegetation remains and in the latter areas non-native weeds greatly outnumber, in bulk, native species of plants. In a few localities close to the edges of the coastal bluffs there remain examples of what appear to be remnants of the native vegetation unaltered. Even these vestiges are annually being encroached upon more and more.

Despite the fact that the pasture lands of today are for the most part vastly changed from the grasslands as they originally existed it still seems worthwhile to record as accurately as possible those avian species which have survived such extensive changes so that comparison may be made in the future when no doubt changes just as great are liable to occur.

As in the case of the coastal brushlands, grass-grown areas are more extensive and extend farther inland in the northern portion of the area due to the more gradual rise in elevation of the land and to the fact that the coniferous forests are more interiorly situated. Within the redwood forested area there is practically no grassland, at least none of sufficient extent to be of any importance as an avian habitat. Sky Meadow, about one mile east of Governor's Camp in the Big Basin, and several small grassy slopes on wooded hills to the north and east of Sky Meadow constitute the only appreciable grassland in California Redwood State Park. These areas, no more than several hundred yards in extent, while forming a definite habitat for certain mammals, were found to be of little importance to birdlife with the exception of the chipping sparrow. The latter species was noted only about the margins of such grasslands.

Riparian.—Two rather separate types of riparian associations occur along the creeks of this region. Within the densely forested portions, azalea (*Rhododendron occidentale*), chain fern (*Woodwardia radicans*), sword fern (*Polystichum munitum*) and other such stream-side preferring species of plants occur in greatest numbers. Of the two types of riparian associations this is the least distinctive, possessing practically no characteristic species of birds. Winter wrens are common inhabitants but by no means restricted to the habitat, occurring very commonly on the lower slopes and in the bottoms of all well-shaded, moist ravines.

Along the lower, more coastal portions of practically all the streams quite a different and more important streamside habitat is present. This is composed principally of trees such as red alder (*Alnus rubra*), broad-leaf maple (*Acer macrophyllum*), cottonwood (*Populus fremonti*) and willow (*Salix* spp.), with dense undergrowth composed of weedy plants and bushy types such as wild rose (*Rosa californica*), blackberry (*Rubus vitifolius*) and poison oak (*Rhus diversiloba*). Species such as downy woodpeckers, belted kingfishers,

russet-backed thrushes, western flycatchers, pileolated warblers, Audubon warblers, song sparrows, golden-crowned sparrows, and white-crowned sparrows were very frequently associated with this habitat.

Marsh.—Only one moderately large marshy area occurs within this region, although there are a number of small tracts of tule and cat-tail growth, of sufficient size to support a number of typically marsh-dwelling species, situated close to the mouths of certain creeks and about reservoirs and ponds.

The only extensive coastal marsh between San Francisco and Monterey bays occurs at the junction of Pescadero and Butano creeks, close to where they enter the ocean. It extends from back of the sand spit, north of the present mouth of Pescadero Creek, in a southeasterly direction for approximately one mile and is about one-half mile in width across its widest portion.

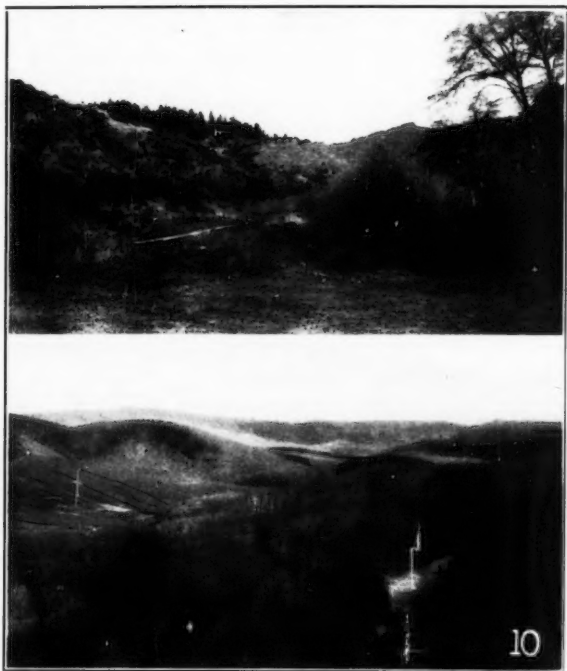


Fig. 9.—Riparian and scattered coastal brush along Gazos Creek, two miles inland from the coast, San Mateo County, California. Photograph taken March 15, 1939.

Fig. 10.—The lower portion of Butano Creek, close to its junction with Pescadero Creek, San Mateo County, California, showing riparian growth, composed principally of alder, cottonwood, and willow, in early spring. Photograph taken March 2, 1938.

The average width is about one-third of a mile. Both Butano and Pescadero creeks wind through the marsh, converging near the western end. The effects of tide are noticeable throughout almost the entire area. In winter the increase in height of the sandbar at the mouth of Pescadero Creek, due to high tides, frequently results in flooding of the entire area.

The following species of plants are of most importance in forming suitable cover for marsh-inhabiting species of birds:

Typha latifolia. Common cat-tail
Distichlis spicata. Salt grass
Scirpus pacificus. Pacific coast bulrush
Scirpus validus. Great bulrush
Atriplex hastata. Fat-hen

Salicornia ambigua. Pickle-weed
Potentilla anserina. Silver-weed
Frankenia grandifolia. Alkali-heath
Grindelia cuneifolia. Marsh grindelia

Decided seasonal changes occur which, to quite an extent, influence the composition of avian populations. By March new cat-tail and bulrush growth is ordinarily well under way with the new stalks two to three feet high and old stalks of the previous year fairly well broken down, yet still providing sufficient cover for ducks, bitterns, marsh wrens and other species relying on this cover for protection. In May the new growth is close to maximum height and the old stalks are completely covered and largely disintegrated. This is roughly correlated with the peak of the nesting season. It is not unusual during the early spring, especially if late rains occur, for the marsh to frequent-

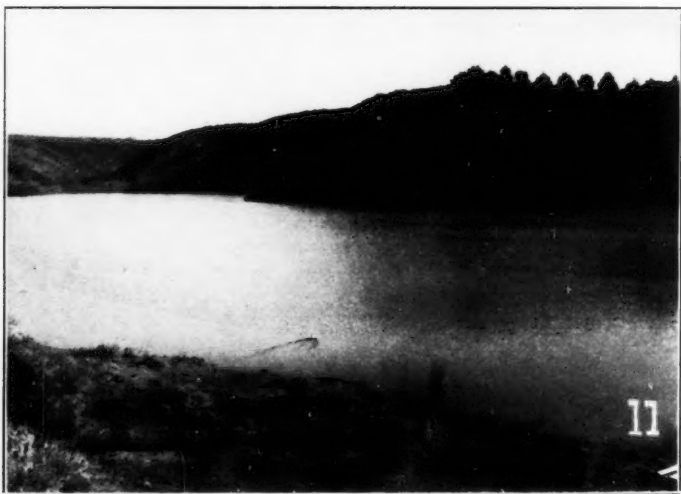


Fig. 11.—Lagoon at the mouth of the Arroyo de los Frijoles, San Mateo County, California. A common loon may be seen swimming away in the foreground. Photograph taken March 2, 1938.

ly be partly flooded. This only tends to delay the breeding season of ground nesting species.

During the summer the marsh is quite dry, except as it is influenced by tide water entering the creek and sloughs. The pickle-weed and marsh grass areas offer, during this time and until late fall, safety to Savannah sparrows and other largely ground-dwelling forms. By the end of August the tules and cat-tails show marked signs of dying down and by the first part of November the stalks are completely dead, although standing and still functioning as suitable bird cover. Early rains in late October and November usually result in flooding the marsh which at this season greatly increases its attractiveness to certain late migrants, such as northern phalaropes, and to wintering waterfowl. This flooded or partly-flooded condition occurs frequently during the early winter until heavy rains or human efforts open the bar across the mouth of the creek.

Both Butano and Pescadero creeks wind through the marsh as do several sloughs which fill up at high tide. These water-courses are lined for a good portion of their lengths in the marsh with tall marsh growth, thus providing good cover for ducks. The western portion of the marsh contains considerably less cat-tail and bulrush growth than the eastern part and is mostly covered with pickle-weed and its associates. The sloughs and the creeks themselves at low tide have exposed mud banks which are attractive to shore birds during the spring and fall periods of migration. In the eastern part of the marsh,



Fig. 12.—The western part of Pescadero Marsh, San Mateo County, California, where pickle-weed is dominant on the alkali flats. Photograph taken March 2, 1938.

where there are extensive areas of tall vegetation, there occur a number of small ponds which are rather inaccessible, from a human standpoint, but due to the protection they are afforded by the surrounding dense stands of cat-tails and bulrushes they prove especially attractive to ducks, coots, bitterns and other species.

Shore.—Shore habitat might well be separated into several subdivisions, including rocky shore, sandy beach and sand dune. As there are approximately twenty-one miles of diversified shore line bordering the western portion of the region included in this study it is only natural that all of these sub-habitats are well represented.

There are very few places where the sea breaks against a solid wall of rock along this particular part of the coast. Such formations, however, are not uncommon to the southward, toward Santa Cruz, and form an additional habitat suitable to species such as pelagic cormorants, pigeon guillemots and black swifts. Although the latter species was not encountered in this region by the writer during the period of this survey [recorded nesting at Berry Creek Falls by Smith, Condor, 1928, pp. 136-138] the former two species were seen on the mainland almost exclusively in these limited situations.

Most of the rocky shore, which includes about one-third of the entire shore line, consists either of sea terraces extending from the base of coastal bluffs well out into the ocean or of low reefs, largely exposed only at low tide. The terraced ledges as well as rocky promontories and proximal offshore rocks mainly provide resting places for gulls, cormorants and rock-preferring species of shore birds. The low reefs, exposed when the tide is out, provide food in the form of small species of mollusks and crustaceans to a good many of the rock-inhabiting species of shore birds as well as to a surprising number of beach-preferring types of sandpipers. Decided preference was



Fig. 13.—Butano Creek at low tide, close to its junction with Pescadero Creek in Pescadero Marsh, San Mateo County, California. Photograph taken January 26, 1938.

shown by certain species, such as the wandering tatter and spotted sandpiper, for rocky shores whose uniformity was broken by the presence of occasional small sandy beaches.

About two-thirds of the shoreline consists of moderately long stretches of sandy beach. Small species of shore birds, such as various sandpipers and small plovers, here were found to secure their main food in the form of sand fleas (*Orchestoidea californiana*). Larger species of shore birds, such as curlews, dowitchers, black-bellied plovers, as well as gulls and scoters, obtained sand-



Fig. 14.—A flooded pickle-weed area in the western part of Pescadero Marsh, San Mateo County, California. Photograph taken November 3, 1938.



Fig. 15.—Sand dunes along the coast, immediately north of Pescadero Creek, San Mateo County, California. Snowy plover and horned larks were two avian species commonly found in such places. Photograph taken December 28, 1938.

crabs (*Emerita analoga*) mainly from these beaches. It is not meant to be inferred that these species obtained all their food from sandy beaches, as a good many of these forms fed elsewhere as well. The two species of crustaceans mentioned above, however, judging from stomach content analyses, constituted the main bulk of food for those species of shore birds frequenting sandy beaches.

Some of the beaches end abruptly at the bases of bluffs, but the majority merge into sand dune areas of varying size and depth. These dunes, as a general rule, are partly grown over with sand-verbena (both *Abronia latifolia* and *A. umbellata*) and shore morning-glory (*Convolvulus soldanella*). Such situations are selected for nesting by snowy plover, possibly also by horned larks. On extremely windy days during the migration periods groups of sandpipers were frequently found to seek protection in the lee of these dunes, where they closely adjoined beach land.



Fig. 16.—A rocky outcropping along the sea coast near Pescadero Point, San Mateo County, California. A number of different species of shore birds as well as gulls and cormorants frequented such places. Photographs taken March 2, 1938.

Species Accounts

Gavia immer (Brünnich)—Common loon

Winter visitant.

Noted on only one occasion. On March 2, 1938, a common loon was seen among some low-growing rushes about ten feet from the water's edge along the shore of the reservoir close to the mouth of the Arroyo de los Frijoles. When the observer came over a small hill, about seventy-five feet distant, into sight of the bird, it immediately made a hasty retreat to the water. This was accomplished in a clumsy manner by repeatedly standing up, taking several steps forward, and landing on its breast. Upon reaching the security of the

water it swam rapidly away, stretching its wings several times and occasionally calling.

Gavia stellata (Linnaeus)—Pacific loon

Probably a winter visitant on open ocean.

Remains of a single individual of this species, estimated to have been dead about one week, was noted on April 27, 1938, on the ocean beach, about three-quarters of a mile south of the mouth of Pescadero Creek.

Gavia stellata (Pontoppidan)—Red-throated loon

Probably a common winter visitant on the open ocean.

The decomposed remains of a red-throated loon were found on May 18, 1938, in Pescadero Marsh. It was estimated that the bird had been dead about three weeks. On May 5, several turkey vultures were noted flying low over the spot.

Colymbus nigricollis (Brehm)—Eared grebe

Common winter visitant; larger ponds and about mouths of large creeks.

Eared grebes were seen between October 7 and May 5 about the mouths of Waddell and Pescadero creeks, in the lagoon and marsh bordered sloughs of the latter creek, and in the reservoir at the mouth of the Arroyo de los Frijoles. On December 28, 1938, approximately 30 individuals were observed, and as many more estimated to be present, in Pescadero Marsh which was flooded, due to a sand bar across the mouth of the creek.

Aechmophorus occidentalis (Lawrence)—Western grebe

Common winter visitant; open ocean, lagoons and mouths of large creeks.

Although individuals of this species were noted from late fall until late spring (May 5, last date seen) greatest numbers were observed during the month of April. While normally a grebe of relatively deep water, certain individuals were on occasions seen diving in water no more than eighteen inches deep, close to shore about the mouth of Pescadero Creek.

Podilymbus podiceps (Linnaeus)—Pied-billed grebe

Winter visitant; ponds and lagoons and mouths of larger creeks.

Pied-billed grebes were noted principally in the fall and early winter months and then in small numbers. The largest aggregation of individuals was observed on October 22, 1937, when 9 grebes were seen scattered about in Pescadero Creek close to its mouth. A single individual was noted in company with a flock of ruddy ducks in Pescadero Marsh on March 15, 1939. This was the only instance in which the species was observed in spring.

Pelecanus occidentalis Linnaeus—Brown pelican

Common visitant, except during breeding season.

Brown pelicans were noted commonly during every month of the year

except February and March, their seemingly complete absence during these two months being attributed largely to their congregating at breeding colonies farther south along the California coast. As a general rule brown pelicans were noted in small flocks, flying parallel with the coast, just beyond the breaker line. These flocks normally contained from 4 to 6 individuals, although flocks containing 7, 12, 14, 19, 21, 31, and 65 were recorded. The latter was the largest aggregation of birds of this species noted flying at any one time. They were observed flying south on October 6, 1938, parallel with and above the coastal bluffs, near Greyhound Rock. Upon passing over a large offshore rock where another large group of brown pelicans was perched, a few of the birds dropped out and came to join those on the rock.

Brown pelicans were occasionally seen on the sandy ocean beaches at low tide or on the sandbar along Pescadero Creek near its mouth. Strangely enough, while pelicans were commonly noted along the coast in this region they were on no occasion observed feeding. Perhaps the absence of protected bays, so favored as feeding sites by members of this species, might account for this.

Phalacrocorax auritus (Lesson)—Farallon cormorant

Irregular visitant.

Farallon cormorants were by far the least abundant of the three species of cormorants known to occur in this region. They were noted during the months of January, April, May, and September, being seen most frequently in Pescadero Creek, close to its mouth, or in the marsh just east of this locality. The greatest number of individuals seen at one time was three.

Phalacrocorax penicillatus (Brandt)—Brandt cormorant

Common resident.

Brandt cormorants were noted more frequently and in greater numbers than any other species of water bird, except perhaps the western gull which was of almost equally common occurrence at all seasons. Smaller numbers, however, were noted during the spring months than at other times during the year. No breeding colonies are known to occur in this region.

Offshore rocks, such as are present south of the mouth of Pescadero Creek, at Pigeon Point, Franklin Point and in the vicinity of Greyhound Rock were invariably found to be inhabited during most of the year by Brandt cormorants. Feeding on the part of members of this species was observed to take place principally in kelp beds close to these rocky, off-shore perches.

Phalacrocorax pelagicus Pallas—Pelagic cormorant

Common resident.

Pelagic cormorants, while common, were not nearly so numerous as Brandt cormorants. They were usually observed in greatest numbers about precipitous off-shore rocks near Pigeon Point and Franklin Point, and in the vicinity of Greyhound Rock. On a ledge, midway between the ocean below

and the top of a sheer bluff, about one-half mile south of Greyhound Rock, what was believed to be a breeding colony of members of this species was observed on May 18, 1938. The birds seen were all in full breeding plumage and, judging from their behavior, appeared to be nesting. It was impossible to be absolutely certain of this, however, as approach for observation could not be made by land to within less than one-quarter of a mile of this point.

Arder herodias Linnaeus—Great blue heron

Common resident; vicinity of marsh land.

Great blue herons were commonly noted in various portions of Pescadero Marsh and about the marshy tract close to the mouth of Waddell Creek. The greatest number of herons of this species seen at one time in the former area was seven. Food was secured principally along muddy sloughs at low tide and about the shallow margins of permanent ponds. On January 26, 1938, however, a great blue heron was observed on a reef at low tide, about one mile south of the mouth of Pescadero Creek. Upon careful approach it was seen to be securing food from various tide pools. At times the surf would almost completely submerge its legs. The presence of the observer disturbed the bird a number of times until it finally flew away out to sea, in a south-westerly direction, disappearing completely from sight as it continued on a perfectly straight course.

Great blue herons were also observed in grassy fields and, in one instance, along the sandy ocean beach between Franklin Point and Gazos Creek. No nests were found, but a grove of eucalyptus trees on the northwest side of Pescadero Marsh was known to be used as a roosting place for herons.

Casmerodius albus (Linnaeus)—American egret

Seemingly resident; marshland.

American egrets were noted a number of times during the years 1936 to 1939, in the vicinity of Pescadero Marsh, principally between February and May. Only one fall observation was recorded. This was on October 7, 1937, when two individuals were seen close together along the bank of a slough. These birds allowed the observer to approach within 40 yards of them and were seemingly indifferent to his presence. This behavior was in marked contrast to that of great blue herons which, in this region, were extremely wary and seldom allowed approach within two or three hundred yards.

No more than two individual egrets were ever noted at a time.

Nycticorax nycticorax (Linnaeus)—Black-crowned night heron

Possible resident in small numbers.

Black-crowned night herons were noted within this region on only three occasions as follows: April 30, 1936, October 7, 1937, and on April 27, 1938. In two instances the birds were flushed from the muddy banks of sloughs in Pescadero Marsh and on another occasion an individual was seen flying down the creek toward the marsh within the limits of the town of Pescadero.

Botaurus lentiginosus (Montagu)—American bittern

Common resident; Pescadero Marsh.

American bitterns were commonly observed in the eastern half of the marsh near the mouth of Pescadero Creek. Here they were inhabitants of the extensive growths of cat-tails and bulrushes in which were located some small ponds. The effect of tide was noticeable here but was largely back water from Pescadero and Butano Creeks.

During the months of April and May bitterns could regularly be heard "pumping" during the late afternoon and evening. On one occasion three individuals were heard, more or less simultaneously, within an area approximately two hundred yards square. In early April bitterns were noted in greatest abundance in the more advanced stands of cat-tails. Later in the season they appeared to be more generally distributed. The earliest in the afternoon that males were heard calling was 3:40 p.m., on May 18, 1938.

Branta nigricans (Lawrence)—Black brant

Migrant; coastwise.

Noted on several occasions in the spring of 1938, and once in 1939. On March 2, 1939, while on a bluff at the mouth of Pescadero Creek, three brant were seen to fly in from the ocean, from the north, and head up the creek. After flying several hundred yards up stream they veered south again down the coast. They were flying at an altitude of about two hundred feet and were heard calling, although not loudly, as they passed over head.

On April 27, 1938, a single black brant was seen swimming in a protected cove within fifty feet of shore along the coast, just south of Pescadero Creek. When the observer approached within one hundred yards it flew out to sea. About one-half hour later, one mile farther south, another brant, possibly the same one, was seen flying down the coast.

On March 15, 1939, a black brant was seen standing on a sandy bank along the north shore of Pescadero Creek about forty yards from where the creek entered the ocean. Upon seeing the observer it walked into the water and swam downstream with the current to a small, kelp-covered, partly-exposed rock at the mouth of the creek where it remained.

Anas platyrhynchos Linnaeus—Mallard

Resident in small numbers; Pescadero Marsh.

Mallards were noted commonly, though never in great numbers, in Pescadero Marsh. The largest number noted was on March 15, 1939, when approximately twenty-five individuals were counted. Preference was shown for the eastern half of the marsh which was predominantly fresh water in nature.

Mareca americana (Gmelin)—Baldpate

Winter visitant in small numbers; Pescadero Marsh.

On December 28, 1938, twenty-four individuals of this species were

observed in flooded portions of Pescadero Marsh. This was the greatest number noted.

Dafila acuta (Linnaeus)—Pintail

Winter visitant; Pescadero Marsh.

Under favorable conditions pintails were the most abundantly represented species of duck in Pescadero Marsh. On December 28, 1938, when the area was flooded, well over two hundred individuals were seen scattered over the open water and it was judged that a good many more were present in the cat-tail and bulrush areas which were not examined.

Netion carolinense (Gmelin)—Green-winged teal

Winter visitant; Pescadero Marsh.

Green-winged teal were noted regularly, but in small numbers, in Pescadero Marsh during the winter season. The earliest noted date of arrival in the fall was September 15, 1938, when a flock of fifteen was observed. The latest date in the spring on which members of this species were seen was April 2, 1936. Restricting themselves, as a rule, to the fresh water portion of the marsh, green-winged teal exhibited decided shyness toward humans, more so than most species of water fowl, and retreated rapidly to the seclusion of dense cat-tail growths even when danger was far distant.

The greatest number of green-winged teal noted at any one time was on March 15, 1939, when about forty individuals were counted. On this day they were noted in greatest numbers at low tide in the western part of the marsh. A few were seen swimming in the creek, but the majority were noted either walking or standing in small groups on mud banks.

On January 26, 1938, a duck hawk was observed to capture a teal of this species from a flock of fourteen that was circling over the marsh. As the hawk made its kill the flock swerved abruptly but flew on silently.

Querquedula cyanoptera (Vieillot)—Cinnamon teal

Common summer visitant; Pescadero Marsh.

The earliest seasonal date of observation for cinnamon teal was April 2, 1936, when about thirty individuals were noted in the evening between 5:00 and 6:30 p.m. They were paired at this time, rarely more than a male and female being seen together. As was true of other fresh water ducks, decided preference was shown for the eastern, cat-tail-covered portions of Pescadero Marsh. Although no nests were found the species undoubtedly bred here.

Nyroca marila (Linnaeus)—Greater scaup duck

Winter visitant; Pescadero Marsh.

Greater scaup were observed only once. On December 28, 1938, a group composed of twenty individuals of this species was seen at a close range, swimming in a flooded area along the margin of a pond in the northwestern part of Pescadero Marsh.

Nyroca affinis (Eyton)—Lesser scaup duck

Winter visitant.

Lesser scaup were seen occasionally, though not in numbers, in the western portion of Pescadero Marsh and in the reservoir near the mouth of Arroyo de los Frijoles.

Glaucionetta clangula (Linnaeus)—American golden-eye

Occasional winter visitant.

The only observation made of any members of this species was on December 28, 1938, in the western flooded portion of Pescadero Marsh. On this date two females were seen at separate points during the morning.

Melanitta fusca Linnaeus—White-winged scoter

Winter visitant.

White-winged scoters were noted practically all year around as a few individuals remained during the summer. They were most numerous, however, in the fall during the latter half of September and the month of October, and in spring during the month of April, although the species was also common in winter. On May 18, 1938, a flock of twelve white-winged scoters, believed to be late migrants, was seen flying north, offshore, opposite Pescadero Point.

White-winged scoters were noted in the following situations: the open ocean offshore, surf, sandy beach, reef, creek mouth and marsh slough. Greatest numbers were seen offshore, either flying or in small flocks on the water. Many individuals, however, were observed feeding along sandy beaches at water line, permitting the wash of the spent waves to move them back and forth. Here they seemed to be in search of sand crabs (*Emerita analoga*). Small groups were often seen just inside or just beyond the breakers. Frequently these individuals had either been disturbed from the beach, had completed feeding, or were on their way toward the beach to feed. In one instance, April 15, 1938, below the mouth of Waddell Creek, three females were observed resting on an offshore reef exposed at low tide.

Individuals were regularly noted during the fall, winter and spring in Pescadero Creek and in the western part of Pescadero Marsh.

Melanitta perspicillata (Linnaeus)—Surf scoter

Common winter visitant.

Surf scoters, like white-winged scoters, were noted practically all year around as a certain percentage of non-migrant individuals remained throughout the summer. At times the impression was had that members of this species were more numerous than white-winged scoters, especially during the spring period of migration. On May 18, 1938, many flocks composed of twenty to thirty individuals were seen flying north, from one-half to one mile offshore, intermingled with great numbers of shearwaters which were also moving in the same general direction.

In habits surf scoters were very similar to white-winged scoters, being found in approximately the same situations. Small groups were frequently noted in Pescadero Creek, usually within two hundred yards of the mouth of the creek. Here they were often noted diving in deep water, apparently feeding. When in shallow water close to shore, however, only the head was submerged.

On April 27, 1938, after spending some time watching a group of eighteen scoters feeding in Pescadero Creek, the birds were disturbed and flew out to sea. Quite a loud whistling sound, seemingly made by the wings, was heard as they rose and passed by the observer on their way out to sea. This flock was mixed as regards sexes. In another instance a flock of five birds, composed of two adult males and three females, was disturbed from a similar situation. The males left first and made a very noticeable whistling sound as they rose. The females left shortly afterwards but no such noise was heard by the observer who was about fifty yards away.

On May 5, 1938, considerable time was devoted to observation upon the feeding habits of a group of nine scoters near Greyhound Rock. They were in the surf and on the wet sand. While little fear of man was exhibited, if too close an approach was made while the birds were on the beach they would fly ten or fifteen yards into the surf and swim away. When undisturbed they would stay around the water's edge in a group. As a wave receded they would waddle toward the next incoming wave, meet it and float in with it. As soon as the wave was partly or nearly spent their heads would be immersed in search of sand crabs (*Emerita analoga*). The heads were kept submerged until the water receded, at which time feeding would cease and they would turn and go to meet the next wave, repeating the process over and over again.

Erismatura jamaicensis (Gmelin)—Ruddy duck

Winter visitant and possible resident.

Ruddy duck were noted both in the marsh and lagoon near the mouth of Pescadero Creek and in the reservoir at the mouth of the Arroyo de los Frijoles. Dates of observation extended from October 6, to March 2. The largest number seen at any one time was on March 15, 1939, when a flock composed of about thirty individuals was observed in Pescadero Marsh. No ruddy ducks were seen during the summer months, although it is possible a few may have been present.

Mergus serrator Linnaeus—Red-breasted merganser

Winter visitant.

Red-breasted mergansers were noted regularly, but in small numbers, between January and May. Usually solitary individuals were observed. They were seen in Pescadero Creek close to its mouth, in Pescadero Marsh, the reservoir at the mouth of the Arroyo de los Frijoles and in the ocean close to reefs along shore. The latest date of observation for this species was May 5, 1938, when a male and female were noted at separate points in Pescadero

Creek. The male flew out to sea shortly after it was sighted. Red-breasted mergansers were found to be extremely wary.

Cathartes aura (Linnaeus)—Turkey vulture

Summer visitant.

Turkey vultures were commonly noted in flight over the coastal portions of this region and they were frequently seen inland soaring over knob-cone pine and chaparral-covered ridges. They were not, however, seen soaring over extensive redwood tracts. Turkey vultures, on a number of occasions, were seen sailing low over the beaches and over Pescadero Marsh. It was thought that they might possibly be in search of dead birds washed in by the tide. On May 5, 1938, several individuals were seen sailing low over a place in Pescadero Marsh where about two weeks later the remains of a red-throated loon was discovered.

The earliest date on which turkey vultures were noted was March 2, the latest date in the fall, October 6.

Accipiter velox (Wilson)—Sharp-shinned hawk

Resident, as well as winter visitant.

Sharp-shinned hawks were noted several times during the months of June and July, indicating a certain resident population. Individuals were seen most commonly in woodlands and along the margins of redwood-Douglas fir forests.

On October 7, 1937, a sharp-shinned hawk was seen to swoop down from a coastal bluff, about one mile south of the mouth of Pescadero Creek, into a group of sanderlings feeding on the beach. The observer's first impression was that a pigeon hawk was striking but second glance soon dispelled such an assumption. It failed to secure its prey although it singled out one sanderling and pursued it for twenty or thirty yards before giving up.

In another instance, on March 5, 1936, in the northern part of San Mateo County Memorial Park, the writer came to a Douglas fir situated on the steep, north-facing slope of a ridge, just a few feet below its crest. A group of pigmy nuthatches, red-breasted nuthatches and chestnut-backed chickadees were heard scolding here. Very shortly thereafter a sharp-shinned hawk appeared suddenly and singled out a chickadee, chasing it through branches of the Douglas fir, across an open space for a distance of ten feet and finally into a bush in which the smaller bird escaped.

Accipiter cooperi (Bonaparte)—Cooper hawk

Possible resident.

Noted but once, on February 27, 1936, when a single individual was seen flying through a Douglas fir forest near the top of a ridge in San Mateo County Memorial Park.

Buteo borealis (Gmelin)—Red-tailed hawk

Common resident; forages over open land or brush.

This was probably the most common species of hawk encountered in this region. Individuals were seen only near chaparral or open grassland, never being associated with densely forested areas.

The ability of members of this species to fight was evidenced on a number of occasions. On March 26, 1936, two miles above the mouth of Gazos Creek, a pair of red-tailed hawks was seen to give chase to a golden eagle that had ventured into their domain. The larger bird flew away without making any attempt to fight back. Similarly, in San Mateo County Memorial Park on April 23, 1936, a red-tailed hawk was seen to attack a golden eagle which was soaring high over a valley. The smaller hawk was seen to dive at the eagle a number of times, calling loudly as it did so. The eagle did not attempt to retaliate but only sought to escape from the attacker. After the larger bird left a second hawk joined the first one. It is of interest to note that a turkey vulture flew close to these birds a few moments later but was not in any way molested. At this same locality on April 2, 1936, a fight between two red-tails was observed for a period of five minutes, during which time they were heard screaming and seen flying at each other viciously. Finally, one of the birds, apparently conceding defeat, flew out of the disputable territory.

On March 18, 1936, in San Mateo County Memorial Park, a red-tailed hawk which had been sailing low over a brushy hillside was seen to dive into the chaparral only to rise a moment later with a small mammal in its talons.

Courtship dives were observed several times during the middle of March, 1936.

Aquila chrysaetos (Linnaeus)—Golden eagle

Resident in small numbers; western section.

Golden eagles were occasionally seen in the western portion of this area, usually where the coastal brushland bordered the redwood-Douglas fir forests. Such places were generally characterized by high ridges and deep canyons which shortly broadened out into wider, cultivated valleys near the coast. In one instance, however, a single individual was seen sailing up the coast, at a height of about two hundred feet above the beach, as though foraging for refuse washed up by the tide. This was just below the mouth of Waddell Creek.

On several occasions eagles were seen to be attacked by red-tailed hawks and in no instance were they seen to fight back. On April 7, 1936, at 3:45 p.m., while observing quail just below the top of a ridge in San Mateo County Memorial Park, an eagle was seen approaching, some distance away. Before it came near the quail retreated from the open grassland, in which they had been feeding, into the nearby chaparral. The larger bird lit in the central part of a solitary Douglas fir which was growing about seventy-five yards from where the quail disappeared. After remaining here for about five minutes it flew back in the general direction from which it had come and disappeared over a nearby ridge. At 4:45 p.m., an eagle, thought to be the same individual noted an hour previous, was seen soaring over this same region.

Circus hudsonius (Linnaeus)—Marsh hawk

Moderately common resident, locally; vicinity of marsh land.

Marsh hawks were seen frequently over nearly the entire length of the open coastal land, being found in greatest numbers in the vicinity of Pescadero Marsh. They were usually noted flying low, or at least within several hundred feet of the ground, over grassy hill-sides, and over extensive sand dune areas, such as near Franklin Point, where a certain amount of swamp land was also present.

On May 18, 1938, the observer was attacked by one of a nesting pair of marsh hawks in Pescadero Marsh. While walking along a levee through a cat-tail grown area a hawk was seen to rise from the top of a fence post about one hundred yards away and fly low and straight toward the intruder. As it came close, however, it rose and passed about seventy-five feet overhead, calling as it did so. After circling about, diving and calling for about five minutes, during which time the observer remained motionless, it flew back and settled on the fence post again. As soon as a motion was made it returned and repeated this performance. This was the only hawk seen in the vicinity during an hour's period of observation and for this reason it was suspected that a female was incubating eggs nearby. On July 27, 1938, in this same vicinity, three marsh hawks, seemingly young of the year, were observed in flight.

On November 3, 1938, many northern phalaropes, present in Pescadero Marsh at this time, showed a definite fear of marsh hawks. Whenever one of the latter would come near a flock of phalaropes the smaller birds would take flight.

Falco mexicanus Schlegel—Prairie falcon

Possible resident.

At Eagle Rock, about noon on April 6, 1936, a prairie falcon was seen flying low over the rocky crest of the peak. It circled briefly over a group of knob-cone pines then disappeared from sight over a rugged section where there were some precipitous cliffs.

Falco peregrinus Tunstall—Duck hawk

Straggler.

Noted on only one day. On January 26, 1938, at 2:00 p.m., a duck hawk was seen to fly north from a bluff overlooking the beach, about one-half a mile south of Pescadero Marsh. At 3:30 p.m., the same day a flock of green-winged teal was observed circling over the marsh. While watching them, as they were flying low and nearby, a duck hawk appeared suddenly from below and grabbed one of the teal. It was rising when the capture occurred. The wings of the hawk made a rushing sound as it stopped in mid-air at the time it caught the duck. The teal, fourteen in number, continued on silently after swerving abruptly. The falcon flew rather heavily toward the coast with its burden and disappeared over a ridge. A fence post was noted beneath the spot where the hawk caught the teal. It is possible that it rose from this site. This was presumed to be the same hawk seen earlier in the afternoon.

Falco columbarius Linnaeus—Pigeon hawk

Rare winter visitant.

On April 2, 1938, a single pigeon hawk was observed flying low over a small, marshy area at the mouth of Gazos Creek.

Falco sparverius Linnaeus—Sparrow hawk

Common resident; open country.

Sparrow hawks were rather widely distributed over the open coastal parts of this region. They were noted most commonly perched on telephone wires along road sides, and hovering over grassy fields and hillsides.

While in this region the species is not definitely known to be migratory, certain seasonal population movements must occur as witnessed by the fact that during the winter months sparrow hawks were much more numerous than in summer.

Lophortyx californica (Shaw)—California quail

Resident; marginal brushland.

Quail were moderately abundant, both along the coast and inland, where suitable expanses of brush were present. The margins of certain tracts of brushlands intermingled with clearings proved most attractive as a habitat for members of this species. Fire trails, cut through extensive brushlands or along the tops of ridges where south-facing brush-covered slopes joined north-facing forested slopes, appeared to increase the amount of available territory suitable to the requirements of members of this species.

Rallus obsoletus Ridgway—Clapper rail

Vagrant or possible resident; Pescadero Marsh.

Shortly after sunset, on the evenings of April 2, and 6, 1936, near the southwestern edge of Pescadero Marsh a clapper rail was distinctly heard calling. It was not, however, until the afternoon of April 9, 1936, that an individual of this species was definitely seen. This bird flushed from the shore of a muddy slough, close to cat-tail growth, when the observer was but a few feet away. It flew about twenty feet and settled down in the cat-tails and was not seen again.

These observations (both sound and visual) aroused considerable speculation as to the possibility of this species being resident here. Careful study of the marsh during this same year and subsequent years failed to result in another sight or sound record of a clapper rail. It is believed, therefore, that the bird noted in April, 1936, was a vagrant that had accidentally arrived here, probably from the marshes about the south arm of San Francisco Bay. It may have arrived during the previous fall or early winter when members of this species seemingly undergo a spreading-out movement. As conditions in Pescadero Marsh appear not unsuitable to clapper rail and might conceivably support a small population of these birds, given the opportunity, this individual may have survived here for some time.

Fulica americana Gmelin—Coot

Resident; ponds, reservoirs and mouths of larger creeks.

While coots were resident in small numbers throughout the summer their population was greatly augmented in the fall of the year by the arrival of large numbers of wintering individuals. On December 28, 1938, more than five hundred coots were estimated to be present in Pescadero Marsh alone. This was the largest aggregation noted at one time in any portion of this area. Although individuals of this species were common in open water a definite preference was shown for the margins of ponds or watercourses where bulrush and cat-tail growth afforded protection. Upon being disturbed or scared they would swim into such cover and disappear from sight.

Charadrius nivosus (Cassin)—Snowy plover

Resident in small numbers; upper parts of sandy beaches.

Snowy plover were noted regularly in limited numbers where suitable conditions prevailed in this region. Gradually sloping beaches backed by sand dune areas were preferred. On April 15, 1938, a pair of snowy plover was seen on the sand dunes back of Greyhound Rock where there was a scanty growth of sand-verbena (both *Abronia latifolia* and *A. umbellata*) and shore morning-glory (*Convolvulus soldanella*). Judging from the behavior of these two birds and their refusal to be driven out of a limited area, they were thought to be nesting. Pairs of snowy plover with similarly established territories were observed on April 27, 1938, in sand dunes about one mile south of the mouth of Pescadero Creek.

On July 19, 1933, several nesting pairs were observed on the upper part of the ocean beach at the mouth of Waddell Creek. In one instance, although neither nest nor young were discovered, a pair was seen to flutter along the sand behaving much as killdeer do in an effort to distract intruders away from eggs or young. About fifty yards away another pair was encountered and a nest consisting of a depression in the sand containing two eggs was found. While each of the pair remained close by they did not display in the manner of the previously-observed birds. Nearby, along the shore of a small lagoon, five snowy plover were seen. They might have been grown young of the year or adults that had finished nesting.

Charadrius semipalmatus Bonaparte—Semipalmated plover

Common migrant; beach land.

Semipalmated plover were noted commonly, although in small numbers, during early May and again in the fall from August 10 to September 6. The greatest number ever noted in one group was six. While frequently associated with certain species of small sandpipers along the ocean shore, members of this species were noted to show preference for areas back a short ways from the wet sand. Along Waddell Beach, on May 5, 1938, this was very well shown. Many groups of two to six semipalmated plover were observed in company with western, least and red-backed sandpipers. In resting and while

feeding, however, they remained higher up on the slopes of the beach, somewhat apart from the sandpipers. When disturbed they would follow the flocks of sandpipers, but could readily be distinguished by the fact that they trailed other members of such a composite flock. On alighting again they would drop down behind the other shore birds and, at the same time, higher on the beach.

Light, at night, had a decidedly confusing and blinding effect upon members of this species. On one occasion an approach with a flashlight was made to within three feet of one individual before it took flight.

A single male, secured on August 21, 1937, one mile south of the mouth of Pescadero Creek, weighed 39.4 grams.

Oxyechus vociferus (Linnaeus)—Killdeer

Resident; grassland, shore and marsh.

Killdeers were noted at various seasons of the year but appeared to be most numerous during the spring. On April 30, 1936, near Franklin Point, a killdeer was observed in a sandy area close to a small swamp. Judging from the consternation it exhibited, because of the observer's presence in this general vicinity, it was believed to be one of a nesting pair.

When noted flying with groups of sandpipers the comparatively limited ability of members of this species to follow the smaller shore birds in mass flight was always apparent.

Squatarola squatarola (Linnaeus)—Black-bellied plover

Common migrant and limited winter visitant; sandy beaches and mud flats.

Black-bellied plover were noted regularly, except between the months of June and August. The species was never numerous but, nevertheless, was of common occurrence. Usually single individuals or two birds were seen together although, occasionally, larger aggregations were noted. On January 26, 1938, a group of nine was seen on a mud flat bordering Pescadero Creek, close to its mouth. This was at 3:00 p.m., when the tide was low. One individual was observed to leave the group, which appeared to be resting, and walk several yards to the water's edge and bathe. After it had completed its bath the other eight birds more or less simultaneously followed its example. The water in which they bathed was two to three inches deep.

During the height of the fall migration, which occurred about the first week of October for members of this species, individuals were sometimes observed regularly about every hundred to two hundred yards along the sandy ocean beach. They were, moreover, at all seasons usually associated with other smaller, sandy beach-frequenting species of shore birds.

While characteristically a species of the sandy beach, black-bellied plover commonly fed also on low reefs, if such were available, when the tide was out. Two individuals were collected on October 7, 1937, on the ocean beach about one mile south of Pescadero Creek. The stomach of one plover contained twelve small periwinkles (*Littorina scutulata*) and remains of sand

crabs (*Emerita analoga*); that of the other a few periwinkles and no sand crabs. On November 3, 1938, at the mouth of Gazos Creek, a plover was seen to dig up a sand crab and run down the beach with it in its bill to avoid a gull and another plover nearby. The observer's approach caused it to fly away with the crab still in its bill.

Aphriza virgata (Gmelin)—Surf bird

Spring and fall migrant; rocky shore.

Surf birds were noted on October 7, 1937, and April 27, 1938, along the coast south of Pescadero Creek. On the latter occasion quite a number of individuals were observed. Groups composed of five, four, twelve, six, two, and five birds were observed along one stretch of rocky shores about one-quarter of a mile in extent. They were noted mostly on rocks partly exposed by low tide and were generally down close to the water's edge. Incoming waves would often cause them to flutter up a little higher, at which times their white rumps and wing-bars were rather conspicuous although, otherwise, the birds blended remarkably well with their background.

Surf birds were found to stay closer to the water than wandering tattlers with which they were frequently associated. They, likewise, often frequented smaller rocks. Compared with other rocky shore-inhabiting species, such as black turnstones, ruddy turnstones and wandering tattlers, surf birds were found to be much less wary and more phlegmatic in their behavior. They permitted close approach and even when disturbed seldom flew more than one hundred yards. Their flight was not straight but slightly zig-zag and occasionally a call note or two was uttered. On alighting they were seldom seen to choose the flat tops of the reefs or rocks but rather the sloping sides, so that they fluttered a bit while securing a footing.

They fed rather slowly, pecking at objects, mostly mussels, on the exposed rocks. The weights of three males secured on April 27, 1938, were 154.9, 160.6, and 151.1 grams. The weight of one female secured at the same time was 197.9 grams. The stomach of the latter (California Academy of Sciences, No. 42686) was found to contain twelve mussels (*Mytilus californianus*) up to 7 millimeters in length, eleven small periwinkles (*Litorina scutellata*), one *Thais lima* and some fragmented shells, gravel and sand. The stomachs of the three males contained as follows: (California Academy of Sciences, No. 42685) six mussels up to 6 millimeters in length, one limpet (*Acmaea* sp.), ten small periwinkles, sand, fragmented periwinkles and mussel shells; (California Academy of Sciences, No. 42687) ten mussels up to 11 millimeters in length, one *Thais lima* and fragmented mussel shells; (California Academy of Sciences, No. 42688) ten mussels up to 12 millimeters in length, a small amount of sand, gravel and fragmented shells.

Arenaria interpres (Linnaeus)—Ruddy turnstone

Probably regular spring and fall migrant in small numbers; rocky shore and beach.

Ruddy turnstones were noted on only one occasion. This was on April

27, 1938, at a point about one mile south of the mouth of Pescadero Creek. Three individuals were seen on this date. They were exceedingly wary and flew away, calling as they did so, before close approach could be made.

Arenaria melanocephala (Vigors)—Black turnstone

Migrant and winter visitant; principally rocky shore.

Black turnstones were noted, not uncommonly, between August 10, and April 27. They were characteristically a species of rocky reefs and kelp-covered, littoral rocks. Their colors blended so well with the dark kelp and rocks that they were often unnoticed on casual observation until they took flight. Field observations made on a small group, composed of six individuals, at Franklin Point on November 3, 1938, were considered rather typical as regards feeding behavior. When first seen the turnstones were methodically turning over small bits of kelp on an exposed reef along shore. Upon being disturbed, however, they flew a short distance out to one of a group of partly submerged rocks in the "breaker belt." Here, as the waves receded, they would rapidly move down close to water line searching for food. When a new wave approached closely they would quickly ascend to the top of the rock and wait for the surf to flow down through crevices and channels in the rocks, at which time they would again follow the receding water in search of food. Sometimes a wave would be sufficiently large as to break completely over the rock. On such occasions they would either fly to another rock or else more or less hover in the air over the same rock until the water receded, then immediately settle down to forage.

On October 22, 1937, a black turnstone was seen in company with a group of nine red-backed sandpipers along the sandy shore of Pescadero Creek, about one hundred yards from its entrance to the ocean. This was at 2:00 p.m. when the tide was high. The turnstone was quite aggressive and would at times force individual sandpipers to move from certain choice feeding spots. It accomplished this by running at them with its neck partly outstretched.

Phaeopus hudsonicus (Latham)—Hudsonian curlew

Spring and fall migrant; sandy beach and mud flat.

Hudsonian curlew were seen on a number of occasions during the periods of migration. They were generally found to frequent extensive sandy beaches, although they were occasionally noted on a mud flat or bar in Pescadero Marsh. Flocks were usually composed of from ten to twenty-four individuals.

The stomachs of two birds collected on May 5, 1938, near the mouth of Waddell Creek, were found to be filled with large sand crabs (*Emerita analoga*). This crustacean was the only type of food these birds were observed to partake of in this region. Sandcrabs were secured by probing in the wet sand. Curlew were seen to exhibit a definite dislike to getting even the lower portions of their legs wet. They would usually stay far enough back so that incoming waves would not quite reach them. When an exceptionally large wave came in they would retreat farther back on the beach, sometimes flying to accomplish this.

When feeding, members of this species usually kept walking along the beach, thus covering considerable distance. On May 18, 1938, a group of ten curlew was observed feeding on a sandy beach just south of Greyhound Rock. During a period of one hour they were observed to traverse the length of this beach, which was three hundred yards, six times. In other words over a mile in a straight line was travelled, although the actual distance traversed in the course of securing food was probably nearer two miles.

The ability of individual birds to signal the approach of danger was noted on May 5, 1938, in this same region. On this date the writer attempted to approach close to a group of about two dozen curlew and some long-billed dowitchers by crawling toward the feeding birds behind the protection of some sand dunes. The first time a close approach was made, but before the observer rose sufficiently to see the birds, one of the curlew flew up. Immediately upon spotting the observer lying prone in the sand, about thirty yards away, it gave a call note. This caused the entire group of curlew to fly away although the dowitchers remained. Twice again during the day this same performance occurred. In each instance a single bird appeared to be responsible for warning the rest.

Actitis macularia (Linnaeus)—Spotted sandpiper

Spring and fall migrant in small numbers; vicinity of rocky shore.

Solitary individuals of this species were noted occasionally. They were seen as a rule on the edges of rocky reefs bordering small sandy beaches where the birds at times were observed feeding. In this regard, as well as in certain other features of behavior, a similarity to wandering tatlers was apparent. When disturbed, spotted sandpipers would usually fly in a small arc and alight on the far side of a nearby reef or shoreline rock, so as to be hidden from sight. Rarely would an individual fly any considerable distance unless forced to do so.

Heteroscelus incanus (Gmelin)—Wandering tatler

Common spring and fall migrant; rocky shore.

Wandering tatlers were noted in the spring, between April 27 and May 13, and in the fall, between August 10 and November 3. The latter date of observation was made in 1938, at Franklin Point, where three individuals were seen. It is possible a few birds may winter here and probable that some non-breeding individuals remain during the summer.

As a general rule no more than three and very often only single tatlers were seen on a reef. Little gregarious instinct was exhibited. On several occasions, however, larger groups were seen. On August 15, 1937, about twenty-five individuals of this species were counted over a distance of several hundred yards. As many as eight individuals were noted flying together in a single file from reef to reef.

Wandering tatlers were strictly inhabitants of rocky shore line. At times, however, they would forage on small sandy beaches very close to the rocks from which they would descend. In such instances they were exceedingly

alert and would fly away calling at the first intimation of danger. Observation showed that tattlers usually frequented the upper parts of reefs or shore line rocks rather than the lower parts, closer to the water, such as are preferred by turnstones and surf birds.

Two females collected about one mile south of the mouth of Pescadero Creek on August 21, 1937, and April 27, 1938, weighed 101.4 and 93.3 grams, respectively, whereas a male taken on the latter date weighed 93.3 grams.

The stomachs of all three contained remains of sandcrabs (*Emerita analoga*), indicating considerable feeding on sandy beaches. The stomach of the male additionally contained remains of a small striped shore crab (*Pachygrapsus crassipes*).

Catoptrophorus semipalmatus (Gmelin)—Willet

Willetts were noted on only one occasion. On January 26, 1938, a flock of about twenty birds was observed to fly up from a mud flat in Pescadero Marsh and head down the coast.

Totanus melanoleucus (Gmelin)—Greater yellow-legs

Spring and fall migrant in small numbers; mud flats.

The earliest fall migrants observed in this region were seen on July 22, 1933; the latest spring migrants were noted on May 18, 1938. Yellow-legs were not common and in no instance was more than two individuals seen at a time. The species, when observed, was generally to be noted about small lagoons, such as are present at the mouth of Pescadero Creek, Waddell Creek and the Arroyo de los Frijoles. Here they would wade along the water's edge probing in the soft mud for food.

Pisobia bairdi (Coues)—Baird sandpiper

Noted as a fall migrant.

On August 16, 1937, a few sandpipers, thought to be of this species, were observed on the ocean beach a short ways below the mouth of Pescadero Creek. On August 10, 1938, at least seven individuals, definitely identified as of this species, were seen along the beach, one-half mile south of Waddell Creek. Three of these were secured to confirm field identification. One group of three was by itself, the others being mixed with flocks of western sandpipers and semipalmated plover. The stomachs of two of the birds taken contained only sand fleas (*Orchestoidea californiana*), while that of the third additionally contained remains of a beetle (*Saprinus sulcifrons*), of the family Histeridae.

Pisobia minutilla (Vieillot)—Least Sandpiper

Common migrant, wintering in small numbers; sandy shore and mud flat.

Individuals of this species were noted between August 10 and May 5. They were usually observed in flocks, often mixed with other shore birds, although it was not unusual to find solitary individuals along small muddy sloughs

in Pescadero Marsh. Occasionally when in company with larger species, such as black-bellied plover, least sandpipers were seen to behave quite independently of the former rather than conform to the more or less uniform flock behavior participated in, in common with other small species of sandpipers. To cite an example, on January 26, 1938, a group of twenty least sandpipers was seen to alight next to a flock of nine black-bellied plover along the muddy shore of Pescadero Creek close to its mouth. The sandpipers rested quietly while the plover bathed. When a second flock of least sandpipers circled over the area the first flock rose in the air instantly and joined them. Shortly afterwards the combined flock lit with the plover. The latter were still bathing and preening.

Only one stomach was examined. This was of a female taken at 6:00 p.m. on August 21, 1937, on the ocean beach one mile south of Pescadero Creek. This proved to be completely empty. The weight of this individual was 19.6 grams.

Pelidna alpina (Linnaeus)—Red-backed sandpiper

Spring and fall migrant; sandy beaches and mud-flats.

The earliest date in the fall on which red-backed sandpipers were noted was October 6, the latest date in the spring being May 5. They were commonly observed during the periods of migration on the mud flats of Pescadero Marsh and close to the mouths of some of the larger coastal creeks as well as along sandy beaches. At low tide they were sometimes seen feeding on small reefs that were backed by sandy beaches. They were frequently noted in mixed flocks with other species of small sandpipers.

Two specimens were collected, one a male weighing 49.3 grams, taken on October 7, 1937, one mile south of the mouth of Pescadero Creek, the other a female weighing 48.7 grams, taken on May 5, 1938, at the same locality. The stomach of the former was empty except for some sand, while that of the latter contained a number of small periwinkles (*Littorina scutulata*).

Limnodromus griseus (Gmelin)—Dowitcher

Migrant.

Dowitchers, while probably of fairly regular occurrence in the spring and fall, were only noted on one day. On the morning of May 5, 1938, a single individual was noted in company with three black-bellied plover on the ocean beach close to the mouth of Pescadero Creek. Later six were seen with a group of twenty-four Hudsonian curlew on the beach south of the mouth of Waddell Creek. This group of dowitchers and curlew was seen to remain together during most of the afternoon.

A female secured on this day weighed 124.4 grams. Its stomach contained remains of some small sandcrabs (*Emerita analoga*).

Ereunetes mauri Cabanis—Western sandpiper

Common migrant; beach and mud flat.

Western sandpipers were one of the most common of the smaller species

of shore birds in this region during the spring and fall periods of migration, being exceeded in numbers only by sanderlings. Seldom, however, were pure flocks of western sandpipers observed, the species usually being associated with other kinds of shore birds. Large numbers were often observed foraging over the mud flats of Pescadero Marsh as well as along the ocean beaches of this region.

A male collected on August 21, 1937, one mile south of the mouth of Pescadero Creek, weighed 19.9 grams. Its stomach was found to contain a number of small sand fleas (*Orchestoidea californiana*). Six females collected on May 5, 1938, at the same locality weighed as follows: 25.2, 25.3, 25.4, 25.7, 27.4, and 27.6 grams. Five males collected at the same time weighed 22.4, 22.9, 26.2, 26.2, and 26.2 grams. The stomachs of these eleven individuals largely contained small snails of the genera *Littorina* and *Bittium* and sand fleas. When collected they were foraging over a small reef which was exposed at low tide as is indicated by the presence of snails in their stomachs. On several other occasions western sandpipers were observed to forage over low reefs.

Limosa fedoa (Linnaeus)—Marbled godwit

Migrant.

This species, while probably of fairly regular occurrence in this region during migration periods, was observed but once. A single individual was seen on the ocean beach, just north of the mouth of Pescadero Creek, at 10:00 a.m. on May 18, 1938. It was probing in the wet sand, close to a group of gulls.

Crocethia alba (Pallas)—Sanderling

Common migrant and winter visitant; sandy ocean beach.

Sanderlings were found to be the most abundant shore birds in this region. The earliest fall date of observation was August 15, and the latest spring date was May 18. The species was commonly noted throughout the winter.

Sanderlings were restricted largely to the open beach where they foraged over the wet sand as the waves receded. When alarmed they were frequently observed to fly to low reefs when these were available and the tide was sufficiently low to expose them. Considerable foraging was also done on these reefs as was attested both by observation and by stomach content analysis. The species was not seen to forage along the banks of the coastal creeks near their mouths nor in marsh land as most of the other species of shore birds were accustomed to do. In one instance, on May 5, 1938, a dead individual was found along the highway near Pigeon Point where it had probably either been hit by a machine or had struck against telephone wires in flight, this was about one hundred and fifty yards from the beach. Occasionally, when it was extremely windy, sanderlings were noted to seek protection on the leeward side of sand dunes back a short ways from the beach proper.

In the middle of the afternoon of October 7, 1937, at a point along the beach about one mile south of Pescadero Creek, a sharp-shinned hawk was

seen to swoop down on a group of feeding sanderlings from a bluff above. Although it singled out a particular bird and gave chase for twenty or thirty yards out to sea as the group took flight, it failed to capture its prey. This alarmed other groups of both sanderlings and red-backed sandpipers within several hundred yards along the beach, causing them to rise and fly out over the ocean. The hawk flew back over the bluff and the sanderlings returned immediately in greater numbers to the point on the beach where the attack had occurred.

During the migration periods sanderlings were usually seen to be accompanied by other small species of shore birds, such as least, western and red-backed sandpipers and black-bellied plover.

A male secured on August 21, 1937, on the beach one mile south of the mouth of Pescadero Creek, weighed 56.1 grams. Its stomach was found to contain a number of small sandcrabs (*Emerita analoga*). A male and two females taken at the same locality the following day weighed 56.7, 58.8 and 56.7 grams, respectively. Their stomachs were also filled with small sandcrabs. Three females collected on October 7, 1937, likewise at this same locality, weighed 58.1, 62.3 and 63.2 grams. The stomachs of two of them were empty except for some grains of sand, while that of the third contained a number of small periwinkles (*Littorina scutulata*). These birds were collected on a low reef.

Lobipes lobatus (Linnaeus)—Northern phalarope

Spring and fall migrant; practically all open bodies of water.

Northern phalaropes were noted irregularly during the periods of migration in this area. In general they were found to be more numerous in the fall than in the spring of the year. A late fall date of observation was November 3, 1938, when hundreds were noted in Pescadero Marsh which was flooded as a result of early rains.

On May 18, 1938, a northern phalarope was observed standing on a dirt road, several hundred yards from the sea shore, at a point about one and one-half miles south of Pescadero Creek. When too close an approach was made it flew up and circled in the air and lit about one hundred yards farther down the road. When a second approach was made it ran a short distance then flew out to sea. This bird may have been injured, although to all appearances it seemed normal.

Larus glaucescens Naumann—Glaucous-winged gull

Common winter visitant.

Glaucous-winged gulls were common in this region from January until the first part of May, the latest date of observation being May 5, 1938. Like California gulls members of this species often frequented plowed or rain-flooded fields in search of food.

Larus occidentalis Audubon—Western gull

Common all year around.

Western gulls were abundant along the coast. at all seasons, although

seemingly less so in June and July than during other months of the year. This seemed attributable to the fact that many of the birds left for breeding areas located to the north and south of this region. Gulls of this species were usually seen flying up and down the coast, perched on offshore rocks, resting on the water or on the beach. Occasionally large numbers were seen congregated on the beaches or on sand bars at the mouths of creeks, often in association with other kinds of gulls.

An adult male collected on August 10, 1938, about one-half mile south of the mouth of Waddell Creek weighed 1199.9 grams. Its stomach contained nothing but a mass of clean fish bones.

Larus argentatus Pontoppidan—Herring gull

Moderately common winter visitant.

Herring gulls were one of the less numerous species of common gulls wintering in the region. They were noted between November 3 and May 5, and were frequently to be seen in groups with other species of gulls on the beaches and sandbars.

Larus californicus Lawrence—California gull

Common winter visitant.

California gulls were noted between September 15 and May 18. This was one of the two most abundantly represented species in this region, during all but the summer season. An individual collected on September 15, 1938, was believed to have just arrived from inland, judging from the contents of its stomach which consisted of a dragon fly and remains of a grasshopper. This was an adult male in fresh winter plumage, except for some of the primaries. Its weight was 680.5 grams.

After the winter rains had set in it was not uncommon to see large groups of California gulls feeding, presumably on earthworms, in a plowed and rain-soaked field.

Larus delawarensis Ord—Ring-billed gull

Winter visitant.

Ring-billed gulls were moderately common, although nowhere as abundant as California or western gulls. The latest date of observation for this species in the spring was May 18, 1938. A juvenile male, collected September 15, 1938, weighed 417.4 grams. Its stomach contained eight sand crabs (*Emerita analoga*) and one sand flea (*Orchestoidea californiana*).

Larus philadelphia (Ord)—Bonaparte gull

Migrant.

Bonaparte gulls were noted on only two days. On May 5, 1938, a group of four was seen flying down the coast, a short ways south of Pescadero Creek, at 11:00 a.m. At 4:00 p.m. four individuals, possibly the same four individuals noted earlier, were seen flying over a small pond at the mouth of

Waddell Creek. On May 18, 1938, seven gulls of this species were seen about the reservoir at the mouth of the Arroyo de los Frijoles. Their weak calls were frequently heard as they flew over the water. Several were swimming in company with a group of northern phalaropes and one was seen resting on a bank along shore.

The absence of any protected bays along this section of the coast was thought to account for the seeming scarcity of members of this species, as they are very common during migration in Monterey Bay not far to the southward.

Larus heermanni Cassin—Heermann gull

Fairly common visitant during the summer and fall.

Heermann gulls were noted between April 14 and October 22. They were present in greatest numbers, however, in the fall of the year. On August 10, 1938, it was estimated that one Heermann gull was seen along the coastal portion of this area to every ten western gulls. On September 15, 1938, Heermann gulls were more numerous in the same region than any other species of gulls. Many pure flocks varying from seven or eight to thirty or more individuals were observed. These were composed of birds of various ages from juvenile to adult. Much of their time was spent on the wet sand, feeding on sand crabs (*Emerita analoga*). Two individuals in juvenal plumage, just beginning the post juvenal molt were secured a short ways from the mouth of Waddell Creek. One of these, a male, weighed 532.8 grams and the other, a female, weighed 503 grams. Two adult males collected at the same time were in nearly complete third winter plumage. Their weights were 548.5 and 620.5 grams. The stomachs of all four birds were filled with sand crabs.

Rissa tridactyla (Linnaeus)—Kittiwake

This species is recorded here on the basis of a carcass found on April 27, 1938, in Pescadero Marsh. It was estimated to have been dead somewhat over a month and was located in a slightly elevated, rush-grown area in the marsh where it seemed unlikely that the tide carried it in. The skeleton, with head lacking, was preserved (No. 42689, California Academy of Sciences).

Hydroprogne caspia (Pallas)—Caspian tern

Migrant.

Caspian terns were noted on three separate occasions flying over the broad portion of Pescadero Creek, close to its mouth, and over the western part of Pescadero Marsh. On April 27, 1938, three individuals were noted together and on both May 5, and July 27, 1938, solitary terns of this species were observed.

Uria aalge (Pontoppidan)—California murre

Transient; principally offshore.

On October 7, 1937, two flocks of approximately twenty-five murrees were seen during the day flying southward offshore at a point about one mile south of Pescadero Creek. Two dead individuals were noted on the beach at this

same locality. On April 15, 1938, a dead murre was seen on the beach near Greyhound Rock and on December 28, 1938, three dead individuals were found washed in at the mouth of Pescadero Creek.

Cephus columba Pallas—Pigeon guillemot

Summer visitant locally, although present offshore at all seasons; frequents ledges on rocky bluffs rising precipitously from the sea.

Pigeon guillemots were noted only during July and August on and about Greyhound Rock at the extreme southern end of the coastal portion of this area. On July 22, 1933, ten individuals were seen on a ledge on the outer part of Greyhound Rock at 6:30 a.m. When close approach was made they flew out singly or in pairs for a distance of approximately one-quarter of a mile, then circled in and either lit on the water for several minutes before circling over the same area or flew close by the rock and out to sea again only to repeat the process. It was believed at this time that they were nesting in crevices on the seaward face of the rock. A pair, thought to have young, was seen at this same locality on August 10, 1938. When approached they flew out from a ledge, one emitting a whistle as it departed. Both lit on the sea about one hundred yards out and swam away from the rock. When some distance off they rose, circled in and lit fifty yards away then swam out again. This performance was repeated a number of times. Once one of the birds was seen to nearly alight on a ledge with something in its bill but, on seeing the observer, it flew out again.

Columba fasciata Say—Band-tailed pigeon

Resident; principally redwood-Douglas fir association.

Band-tailed pigeons were noted principally on the slopes of canyons, forested with redwood and Douglas fir. Most of their time was spent in the upper parts of these trees. Occasionally, however, they were seen in the lower, western, coastal area. In one instance on April 30, 1936, a flock of over forty birds was observed in cottonwood and eucalyptus growth bordering Pescadero Creek about one mile from its mouth. The largest number of pigeons observed in any flock was forty-four. Flocks usually consisted of from ten to twenty individuals.

Zenaidura macroura (Linnaeus)—Mourning dove

Summer resident; preferably open land.

Doves were noted fairly often during the summer months in the western portion of this region, where open fields and meadow lands were present. The earliest date on which this species was noted was March 2. Like certain other avian species, such as sparrow hawks, shrikes and meadow larks, telephone wires when present were commonly used for perching by doves. On one occasion, May 1, 1936, two mourning doves were seen walking on the highway at the western end of San Mateo County Memorial Park. This was in the redwood forest, a most unusual place for doves. Toward the latter part of the summer small flocks composed of as many as one dozen individuals were often noted.

Tyto alba (Scolopi)—Barn owl

Resident.

Although barn owls were probably resident in numbers over many parts of this region, the species was observed but once. At dusk on May 5, 1936, a single individual was seen flying over the western part of the town of Pescadero.

Otus asio (Linnaeus)—Screech owl

Resident.

Screech owls were heard a number of times at night along the coastal parts of this area. On July 22, 1933, a screech owl was heard calling around 10:00 p.m. from a grove of Monterey pines close to the mouth of Waddell Creek. The calls were given after four or five minute intervals.

Bubo virginianus (Gmelin)—Horned owl

Common resident; forested and wooded regions.

This appeared to be the most widely represented and abundant species of owl present throughout this area. Horned owls were noted in densely forested portions, in woodlands and even in eucalyptus groves along the coast.

From the end of February until April it was not uncommon to hear individuals calling as early as the middle of the afternoon. On May 23, 1935, close to Sky Meadow, a horned owl was heard hooting at 6:50 p.m. from the upper part of a tall redwood. It was answered shortly afterwards by another individual, thought to be about one-quarter of a mile away. This continued for some minutes, during which time the calls of the second bird sounded progressively louder, as though it were approaching. At 7:05 p.m. the second owl was seen to fly overhead, at a height of about two hundred feet, and alight on a dead branch of a tall redwood growing next to the tree in which the first bird was perched. Immediately upon alighting it was attacked a number of times by an acorn-storing woodpecker. During this period of observation another pair of horned owls was heard calling in the distance. Both pairs were heard regularly up to 7:30 p.m., at which time the observer left.

On March 5, 1936, in San Mateo County Park, a pellet believed to belong to one of this species was found on a redwood log in the forest. Remains of a meadow mouse (*Microtus californicus*) were positively identified in it.

Glaucidium gnoma Wagler—Pigmy owl

Probably resident; forested areas.

While this species is probably resident in fair numbers in densely forested portions of this area its presence was recorded only once. On May 23, 1935, near Sky Meadow, a commotion was heard among a group of chestnut-backed chickadees at 8:00 a.m. Investigation showed a pigmy owl as the cause. The small owl was continually harassed by the chickadees which flew about calling excitedly but never touching the larger bird. When first seen it was perched in a coast live oak about thirty feet above the ground. After several minutes

it flew to another oak about fifty feet away where it was followed by its attackers and where it remained for five minutes. From here it flew up into a densely foliated portion of a large redwood, about one hundred feet distant, where it eluded the smaller birds.

Phalaenoptilus nuttalli Audubon—Poor-will

Summer visitant; gravelly or rocky clearings on chaparral slopes or tops of ridges.

The earliest date on which evidence of this species was noted was April 15, 1938. On this date a dead individual was found during the morning, on the highway just south of the town of Pescadero. An examination showed it to have been dead about thirty-six hours. Poor-wills were seen commonly in the evening during the summer along roads leading through chaparral and on barren, rocky, open spaces in chaparral. On June 21, 1935, while driving up the south side of China Ridge from Big Basin a poor-will was seen on the highway, at 7:45 p.m. When the car approached within twenty-five feet it flew up and more or less fluttered fifty feet farther on before it settled on the highway. As the car continued toward it the same performance was repeated several times, the bird appearing loathe to leave the road. It finally retired to the side of the highway and was passed. The eyes shone dull red when facing the headlights of the car.

Chaetura vauxi (Townsend)—Vaux swift

Summer visitant.

The earliest seasonal date of observation for this species was April 14, 1936, when a single individual was seen flying over a ridge in San Mateo County Memorial Park. Vaux swifts were noted frequently, although in small numbers, during the summer. They were usually seen flying over the tops of inland ridges or high over forested canyons. When foraging in the air over ridges, swifts invariably flew at a considerably higher elevation than purple martins. A twittering call note was heard almost continually when they were in flight. No nests were located although the species undoubtedly breeds in this region.

Aëronautus saxatalis (Woodhouse)—White-throated swift

Transient or possible resident.

Two white-throated swifts were noted flying over the top of Eagle Peak on July 17, 1935. This is the only occasion on which the species was noted. These birds were thought to be transients, although it is possible a breeding colony might have been located in the southern portion of the region or nearby as there are several precipitous, rocky cliffs of considerable size hereabouts.

Calypte anna (Lesson)—Anna hummingbird

Resident.

Anna hummingbirds were not common within the region studied, being greatly outnumbered during the summer months by the Allen hummingbird.

Selasphorus alleni Henshaw—Allen hummingbird

Summer visitant; principally chaparral associations.

Allen hummingbirds were present in numbers from the latter part of February through the summer in this region. They were primarily associated with chaparral tracts, both inland and along the coast, although a certain number were found to occur in oak-madrone associations. Members of this species seemed very dependent upon bush monkey flower (*Diplacus aurantiacus*). The presence of this plant was almost invariably an indicator of the presence of Allen hummingbirds. The latter relied to a large extent upon the flowers of the bush monkey flower for food, especially during the summer when flowers were scarce in the chaparral. California figwort (*Scrophularia californica*) was probably second in importance as a food plant.

Megaceryle alcyon (Linnaeus)—Belted kingfisher

Resident; vicinity of water courses or bodies of water.

Belted kingfishers were noted along the larger streams, both coastwise and inland. They were, however, seen much less frequently along streams in redwood forested areas, preferring the more or less open coastal portions of these water courses, where overhanging trees such as cottonwoods offered suitable perches. Posts and stumps sticking out of the water in reservoirs and lagoons were particularly attractive to kingfishers.

Colaptes cafer (Gmelin)—Red-shafted flicker

Resident; widely diversified habitats.

Red-shafted flickers were found in all but a very few of the avian associations present in this region, being absent from dense redwood groves and marsh land as a rule. It is probable that on occasions flickers may even frequent these habitats. They were common in woodlands, Douglas fir forests, both coastal and inland chaparral, open fields, on beach bluffs and were even observed at times on sand dunes.

Call notes commonly associated with the breeding cycle were heard most frequently during the months of April and May. On April 2, 1936, in San Mateo County Memorial Park, a red-shafted flicker was noted calling from the upper portion of the trunk of a Douglas fir. Shortly afterwards it was answered by another individual of this species in a tree about two hundred yards away. The latter then flew to the tree in which the other bird was located and lit near it. No activity was apparent for the next five minutes and then one of the two flew to the tree from which the second individual had come. Upon alighting it immediately began calling and drumming, more or less alternately. The other bird called also but was not heard to drum. This calling and drumming was kept up for the following half-hour until the observer left.

Balanosphyra formicivora (Swainson)—Acorn-storing woodpecker

Common resident; throughout forested sections.

A combination of redwood, Douglas fir and oak, fairly well spaced, proved

most suitable for members of this species. Decided preference was shown for tall dead trees or large redwoods which were dead or leafless at their tops. While dead trees were generally selected for the storing of acorns, in many instances these were stored in the bark of living redwoods. Storage holes were rarely found within fifty feet of the ground. Frequently they were near the tops of tall trees, as high as two hundred feet. The acorns stored were principally those of tan oaks and canyon live oak. Many hulls were found beneath these storage trees during the spring months.

During June and July considerable insect food was secured by this species of woodpecker. In one instance, on July 11, 1935, on Pine Mountain, eight acorn-storing woodpeckers were observed at once, perched on the tops of tall dead trees and the dead tops of living redwoods. During a short period of observation they were seen to fly out regularly to secure insects on the wing, returning to the same perch or one located nearby. Occasionally they would fly out as far as one hundred feet. As many as three "fly-catching" woodpeckers were noted in a single tree at one time.

On May 23, 1935, at 7:05 p.m. along the margin of Sky Meadow, an individual of this species was observed to make repeated attacks on a horned owl which alighted on a dead branch at the top of a tall redwood in which the woodpecker was perched.

Dryobates villosus (Linnaeus)—Hairy woodpecker

Common resident; redwood-Douglas fir association.

Hairy woodpeckers were observed at all seasons of the year in forested parts of this region. Although they were noted most frequently on Douglas firs and tan oaks, individuals were often noted on redwood trunks and limbs as well as alder and other species of forest trees.

Dryobates pubescens (Linnaeus)—Downy woodpecker

On the morning of April 2, 1936, a downy woodpecker was seen and heard calling on the trunk of a cottonwood tree along Pescadero Creek close to the southwestern limits of the town of Pescadero. This was the only instance in which this species was observed.

Myiarchus cinerascens (Lawrence)—Ash-throated flycatcher

Moderately common summer visitant; hard chaparral and margins of wooded areas.

Ash-throated flycatchers were commonly observed in inland chaparral occurring principally along the margins of such areas adjacent to woodland. Dead brush was mainly relied upon for perching sites. It was not uncommon, however, to see members of this species on dead stumps and posts or even on the lower branches of oaks and madrones in woodland areas and on occasions on the dead tops of redwoods along the edges of forest land.

On July 10, 1935, on China Ridge a pair of ash-throated flycatchers were observed with a young of the year. Although the latter appeared as proficient

at foraging as the adults it would invariably beg for food by fluttering its wings and giving a whining note whenever the parents came near.

Sayornis nigricans (Swainson)—Black phoebe

Resident; coastal parts, vicinity of ponds or streams.

Black phoebes were noted commonly throughout the year in the western part of this region but were more widely distributed during the winter months. At this season they were especially common along the beaches where they were often noted perched on piles of driftwood from which they would sally forth after flying insects. During the spring and summer months they were more restricted to the vicinity of ponds and watercourses.

On April 15, 1936, near Pescadero, an individual was seen carrying nesting material. On April 27, 1936, near the western end of the town of Pescadero one of a pair of black phoebes was seen to fly down to the creek bank, take up a bill full of mud and fly to the roof of a nearby shed. Here it perched for several seconds then flew to a ledge beneath the eaves of a house close by. Closer inspection showed that a platform of mud had been constructed on this ledge.

Sayornis saya (Bonaparte)—Say phoebe

Winter visitant; marsh and open fields.

Say phoebes were noted between October 6 and March 15, in the western portion of this region. Members of this species were never numerous but solitary individuals were often noted during the winter months, perched on fences in open fields or on posts or bushes which rose above the pickle-weed growth in marsh land.

Empidonax difficilis Baird—Western flycatcher

Summer visitant; redwood-Douglas fir and woodland associations.

Western flycatchers were noted in the spring as early as March 26. They were common inhabitants of the redwood forests and rather dense woodland areas, where they were noted most often in the lower branches of trees. Western flycatchers were characteristically a bird of well-shaded parts of the forest. On Waddell Ridge, on June 14, 1935, young, not long out of the nest, were observed being fed by their parents.

Myiochanes richardsoni (Swainson)—Wood pewee

Summer visitant; woodland.

Wood pewees were present during the summer months in the eastern part of this region, being restricted principally to wooded regions. They were not found in densely forested situations.

Nuttallornis mesoleucus (Lichtenstein)—Olive-sided flycatcher

Summer visitant; forested or wooded regions.

Olive-sided flycatchers were noted in the spring as early as April 23.

Individuals of this species were found most frequently along the margins of forests or in woodlands where they perched on the tops of tall trees. Dead trees which rose above the general level of the surrounding forests were especially selected. A preference was, likewise, exhibited for such trees on slopes, rather than those on flat land.

On China Ridge, on July 10, 1935, a pair of olive-sided flycatchers and a young of the year were seen about the tops of some tall knob-cone pines, close to both an oak-madrone woodland area and a Douglas fir-redwood forest. One of the adults was observed carrying an insect in its bill but it was not determined whether or not this was for the juvenile. All three finally flew over to the forested area.

Otocoris alpestris (Linnaeus)—Horned lark

Resident; open fields and sand dunes.

Horned larks were noted principally in the extensive sand dune areas extending north from the mouth of Pescadero Creek and in and along the margins of fields cultivated for truck garden crops along the coast. Plowed fields proved especially attractive to members of this species although this attraction sometimes proved detrimental. In the spring of 1938 horned larks were noted in pairs, by the middle of April, in the fields that had been plowed the previous fall in the vicinity of the town of Pescadero. All indications were that nesting was under way. During the first week in May, however, most all of these fields were plowed again. Immediately following this horned larks in this vicinity were noted in flocks composed of five or six birds. It would seem as though this disturbance had completely disrupted the breeding cycle for the time being.

Iridoprocne bicolor (Vieillot)—Tree swallow

Migrant; coastwise.

Tree swallows were noted only as a spring migrant in this sector, during the month of April and in early May. They were usually noted flying high over the coastal valleys and marsh lands or, occasionally, low over creeks or perched on telephone wires. On April 15, 1936, it was estimated that there were literally thousands of tree swallows sailing high over Pescadero Marsh in the late afternoon.

Riparia riparia (Linnaeus)—Bank swallow

Summer visitant.

On July 22, 1933, bank swallows were commonly noted flying up and down the beach near the mouth of Waddell Creek. It seemed likely that a colony was located in this region, possibly on Año Nuevo Island where they have been reported nesting in the past. While no other field note entries were made for this species during the period of this study, it is highly probable that bank swallows regularly occur in the southern coastal part of this area during the summer.

Stelgidopteryx ruficollis (Vieillot)—Rough-winged swallow

Possible summer visitant.

On May 7, 1936, a number of rough-winged swallows were observed flying alongside the cliffs and steep-sided gullies in the vicinity of the mouth of Pescadero Creek. Possibly a small number of individuals remain during the summer within this region.

Hirundo erythrogaster Boddaert—Barn swallow

Summer visitant.

Barn swallows were common during the summer months in the western part of this region, especially in the vicinity of barns and bridges. The earliest date on which they were noted was March 26. On their arrival in the spring, members of this species were frequently noted in flight with large numbers of tree swallows over meadow land or marshy areas along the coast.

On April 20, 1936, a number of barn swallows were seen flying low over Pescadero Creek, just west of the town of Pescadero. Very often they would contact the surface of the water as though drinking. During May and June swallows of this species were noted collecting mud for nests at a number of different localities.

Petrochelidon albifrons (Rafinesque)—Cliff swallow

Summer visitant.

Cliff swallows were commonly noted during the summer, particularly along the coast. Here they were seen flying over beachland, marsh, meadow and especially in the vicinity of barns. Telephone wires were very frequently used for perching sites.

Cliff swallows were noted carrying mud for nests at a good many localities between April 6 and June 25. The margins of small ponds and puddles on dirt roads were preferably selected for this purpose, although the muddy banks of creeks were also used for this. When in the act of collecting mud, the wings were held up in the air and beaten rapidly, even though the feet were resting on the ground. In the late afternoon of May 13, 1936, several pairs of swallows were observed depositing mud beneath the eaves of a house in Pescadero.

On April 27, 1938, many cliff swallows were noted flying over Pescadero Marsh, some skimming low over the water. One individual that happened to be flying close to the observer was seen to fly so low that it frequently touched the water with its bill. Its mouth was kept open most of the time and to all appearances it was drinking. On August 10, 1938, while observing cliff swallows along the ocean beach about one-half mile south of Waddell Creek, individuals that were flying low were, on several occasions, seen to alight momentarily on the sand.

Progne subis (Linnaeus)—Purple martin

Summer visitant; both inland and coastwise.

Purple martins were commonly noted in summer, flying over the higher ridges in the eastern parts of this region. Very often they would skim low

over the tops of the ridges, within several feet of brush, only to sail out high over adjacent canyons, rarely descending in altitude. They would, occasionally, more or less stop in mid-air and hover. Most of the twittering made by members of this species was heard to come from perched individuals. The dead, uppermost limbs of tall redwoods situated on the upper slopes of canyons were most commonly used as perching sites.

Occasionally martins were noted flying over the ocean beach, especially in the southern part of this area where high, precipitous bluffs occurred back of the beach.

Cyanocitta stelleri (Gmelin)—Stellar jay

Common visitant; principally redwood-Douglas fir forest.

The presence of humans, as in camping areas, seemed to prove particularly attractive to members of this species. The reason for this, obviously, was the food which campers and picnickers were always willing to give these birds.

Their presence in abnormal numbers around camping areas appeared to be definitely correlated with a reduction in the numbers of small passerine birds in such places, especially during the nesting season. On more than one occasion jays were seen hunting for the nests and young of smaller birds, much to the displeasure of the latter. Ground nesting species, such as the Oregon junco, appeared particularly wary and excited when a jay was in the vicinity.

On May 22, 1935, along the East Fork of Waddell Creek in a redwood-Douglas fir forest a Stellar jay was observed carrying nesting material. By the middle of June many young, just out of the nest, were observed in California State Redwood Park.

Apelocoma californica (Vigors)—California jay

Common resident; chaparral and oak-madrone woodlands.

During the breeding season members of this species were noted most frequently near low-growing, live oaks which were preferred as nesting sites. The first signs of nesting activity were noted early in April when the jays became extremely wary and quiet. On April 14, 1936, in San Mateo County Memorial Park, a pair of jays was observed building a nest near the top of a small canyon live oak, about fifteen feet above the ground. On this date only a meager platform had as yet been constructed. When visited on the morning of April 28, not a jay was in sight and on climbing the tree, the nest was found to be completed. It was well-protected above from rain and direct sunlight by a dense clump of leaves. The base and main bulk of the nest was composed of small twigs, and the cup was neatly lined with rootlets. No eggs were present. On returning later in the day and remaining quiet and concealed for about ten minutes, the pair was seen to fly quietly, near the ground, from some brush not far distant, to the nest tree. Here they gave some low buzzing notes and, after fifteen seconds, one of the birds flew to the top of a nearby madrone where it remained quiet and motionless for fifteen minutes. It then flew back to the nest tree. On May 1, the female, presumably, was found

sitting on the nest. When she was flushed off, the other member of the pair appeared. Both birds registered considerable alarm while the nest was being examined. Two eggs were present. Upon returning to the nest on May 14 it was found to have been deserted, leaves and debris covering the two eggs.

Corvus corax Linnaeus—Raven

Transient; coastwise.

Ravens were noted on only two occasions. On April 2, 1938, three ravens were heard calling and seen flying over a ridge just south of Pescadero Marsh. On April 15, 1938, two ravens were observed circling about the summit of a small, rocky hill about one mile south of the above-mentioned locality, near Pebble Beach.

Corvus brachyrhynchos Brehm—Crow

Transient.

On March 2, 1938, a single crow was observed in a plowed, rain-soaked field with a group of glaucous-winged and California gulls. This individual was extremely wary, much more so than the gulls, and when approached flew a considerable distance away long before the gulls made any effort to leave.

Penthestes rufescens (Townsend)—Chestnut-backed chickadee

Common resident; forest and woodland.

Chickadees, while typical of the redwood forest, were often found in other situations. They were frequently encountered in the oak-madrone forests, in Monterey pine forests along the coast, in willow and alder bordering creeks and even in brush, such as chaparral broom and ceanothus, where it was not situated far from trees.

This was one of the earliest nesting species in the region. Along Pescadero Creek, about one mile from its mouth, on March 20, 1936, a pair of chickadees was observed in some cottonwoods carrying nesting material. On March 26, 1936, on Butano Ridge, a pair of chickadees was seen carrying moss into a nest hole situated about thirty feet up in a dead Douglas fir. This tree was located on a slope where there was a change from woodland to chaparral and was out in the latter association. On May 29, 1935, a young individual, as yet unable to fly any distance, was found on the ground beneath a large Douglas fir in Governor's Camp. The parents exhibited great concern when the young one was picked up and placed on a branch. On this same date one member of another pair, observed near Sky Meadow, was seen carrying a caterpillar in its bill, presumably for young.

At 8:00 a.m. on May 23, 1935, near Sky Meadow, a group of chickadees was observed annoying a pigmy owl which was perched well up in a canyon live oak. The smaller birds, however, were not seen to touch the owl, although they flew about it and called excitedly. In the late afternoon of March 5, 1936, near the crest of a ridge in San Mateo County Memorial Park, a group of chestnut-backed chickadees, pigmy nuthatches and red-breasted nuthatches was heard scolding loudly in a large Douglas fir. A very few moments later

a sharp-shinned hawk was seen to chase a chickadee through the foliage of the tree and across an open space of about ten feet into a bush in which the smaller bird escaped.

Psaltriparus minimus (Townsend)—Bush-tit

Common resident; woodland.

Bush-tits were most frequently associated with live oaks. Members of this species, however, were often noted foraging well out in chaparral and one pair was even found nesting in lupine, close to the beach.

Although occasional pairs were noted prior to the latter part of March, most of the birds seen up to this time were in flocks. On April 2, 1936, in San Mateo County Memorial Park, a pair of bush-tits was observed building a nest in a coast live oak. The oak in which they were building was one of a small group situated in a semi-open place on a hillside, between a redwood-Douglas fir forest and some chaparral. The nest, which was more than half built, was located about twelve feet above the ground on the outer part of one of the lower branches of the tree on its down-hill side. The pair was seen to make repeated trips after small fibers of bark and leaves. They were never noted more than sixty yards away from the tree, often going into low brush in search of nesting material. Seldom was any noise made when they were close to the nest. Two orange-crowned warblers and a pileolated warbler were seen in this same tree a number of times. In the late afternoon of April 7, this nest was still under construction.

In another portion of the Park, on April 28, 1936, a nest was found. This was situated near the top of a small canyon live oak, about fifteen feet above the ground. This tree was growing on a slope and was adjacent to a patch of chaparral broom and poison oak on one side and a redwood forest on the other. The nest appeared to be almost complete although the birds were still carrying nesting material. A week previous to this a pair of bush-tits had been seen with nesting material near this tree. The nest was composed largely of moss, lichens and plant fiber. No attempt was made on April 28 to peer into the nest as the observer presumed, perhaps erroneously, from the fact that the pair was still industriously carrying building material that no eggs had as yet been laid. Sixteen days later, on May 14, when examined, it contained six newly hatched young and one egg yet unhatched.

A pair of bush-tits observed near Franklin Point on April 30, 1936, was believed to have a nest in a dense clump of willows growing out in the sand dunes among lupines. On May 13, 1936, a nest belonging to a pair of bush-tits was found in a lupine bush along an old road close to the mouth of Pescadero Creek. The nest was four feet above the ground and well screened from view by dense foliage. It was composed mostly of lichens and cottony material and contained seven partly incubated eggs. The adults remained close by while it was being investigated. Two days later when examined it appeared the same. It is of interest to note that no trees were growing within about a mile of this locality.

In San Mateo County Park, on May 14, 1936, two more bush-tit nests

were located. Each was situated in a live oak bordering a redwood-Douglas fir forest and each was about ten feet above the ground. Both nests contained young which were being fed regularly by the parents. On this same day a family group composed of two adults and several young was seen near the top of a ridge in the park.

Sitta canadensis Linnaeus—Red-breasted nuthatch

Winter visitant; principally Douglas fir association.

The red-breasted nuthatch was commonly observed during the winter season, being confined largely to areas where Douglas firs were growing. Individuals were noted most frequently foraging over the trunks and limbs of these trees and occasionally were seen searching over the cones for food material. The latest date of observation for members of this species was May 1.

Sitta pygmaea Vigors—Pigmy nuthatch

Common resident; knob-cone pine and redwood-Douglas fir associations.

Pigmy nuthatches were noted in small flocks during all of the year except the breeding season. They were typically associated with knob-cone pines in this region, although they were frequently observed in redwood and Douglas fir forests. When foraging, member of this species spent most of their time on the uppermost limbs of the taller trees. Rarely was a flock restricted to one tree, usually being distributed over several trees at a time. Under such circumstances individuals were almost constantly heard giving call notes.

On July 11, 1935, on the northeastern slope of Pine Mountain, young pigmy nuthatches were observed on the trunk of a Douglas fir, being fed by their parents.

Certhia familiaris Linnaeus—Brown creeper

Resident; redwood forest.

Creepers were noted commonly, though never in numbers, in the denser portions of redwood forests. On occasions they were observed on live oaks. Individuals were restricted almost entirely to the trunks and larger branches of these trees, foraging over the bark.

Chamaea fasciata (Gambel)—Wren-tit

Common resident; brushland.

Along the coastal portion of this area chaparral broom sagebrush and coffee berry provided suitable cover for wren-tits. This species appeared to be somewhat more numerous, however, on the warmer, more inland ridges which were overgrown with manzanita, chamise and chinquapin. Cut-over areas invaded by ceanothus, as well as new second growth redwood forests where manzanita, ceanothus and chaparral pea were abundantly intermingled, proved equally inhabitable to members of this species. Although wren-tits were heard giving territorial song throughout the year, they were heard most frequently between March and July.

Cinclus mexicanus Swainson—Dipper

Probable resident; streams.

Although dippers undoubtedly occur along the larger creeks, such as Pescadero, Gazos and Waddell creeks, the species was noted only once, on Butano Creek. Here on March 26, 1936, near Butano Falls, an individual was observed feeding along partly submerged rocks in small rapids.

Nannus hiemalis (Vieillot)—Winter wren

Common resident; redwood forest.

Winter wrens were noted only in the densest portions of redwood forests, usually in canyon bottoms. Here they inhabited dense undergrowth and tangles, often along small stream courses. Individuals were heard singing as early as the latter part of February. Young, not long out of the nest, were observed foraging with their parents about a culvert along the West Fork of Waddell Creek on June 11, 1935.

Thryomanes bewicki (Audubon)—Bewick wren

Common resident; principally in chaparral.

Bewick wrens were abundant both in coastal and inland hard chaparral, as well as in marginal woodlands where considerable underbrush was present. Young second growth redwood forests, in which there was an abundance of ceanothus, proved equally inhabitable to members of this species.

Singing individuals were heard regularly from the end of February until the middle of July. A nest containing four young birds was found near the mouth of Pescadero Creek on May 7, 1936. It was located in a hole about four feet below the top of a bluff which rose precipitously to a height some thirty feet above the creek. There was no vegetation growing immediately around the nest hole other than a very small lizard-tail plant, not over two inches high. Five feet below this, however, there was a dense growth of brush, composed mainly of lizard-tail and lupine. The nest was eight inches in from the mouth of the hole, which was one and three-quarters inches in diameter, and was down in a depression so that the top of the nest was flush with the floor of the hole. It was made of small lupine stems and lined with plant fiber and down. Whenever a stick was poked near the young they invariably opened their mouths. Both parents were observed carrying food. An examination on May 12, showed the young to be fully feathered and about ready to leave the nest. Two of them when first seen were close to the mouth of the hole. They immediately scurried in when the observer approached closely. The following day the young were out of the nest and scattered about in nearby clumps of lizard-tail, both above and below the nest hole. They were being fed by the parents and, when receiving food, could be heard calling a considerable distance away. On May 15, they were also observed being fed in this immediate vicinity.

A nest was found in San Mateo County Memorial Park on May 13, 1936. It was situated in a cavity near the bottom of a wood rat nest about

twenty feet above the ground in a coast live oak. The nest was eight inches back from the entrance to this tunnel-like cavity and contained four young which were fully feathered and almost ready to leave.

Telmatodytes palustris (Wilson)—Long-billed marsh wren

Resident; marshland.

Marsh wrens were present throughout the year in Pescadero Marsh and in the small marsh at the mouth of Waddell Creek. While the call notes of members of this species were one of the most conspicuous features of these two marshes the year around, song was restricted largely to the period from March to August.

The months of April and May were those in which the greatest nesting activity was noted in Pescadero Marsh, although nestlings were observed even in the latter part of July. Nests were constructed in cat-tail and bulrush areas. During April many solitary individuals, presumably males, were noted building nests in small patches of the previous year's dead bulrushes (*Scirpus validus*). These patches were situated along sloughs or ramifications of Pescadero Creek and usually were not more than five by fifteen yards in dimensions. These males would often have three or four freshly constructed nests within their territory. In such instances, the new growth of bulrush was short, being less than a foot in height on the average. The nests, of course, were placed on the dead stalks and usually were about two and one-half to three feet above the mud. At this same time new cat-tail (*Typha latifolia*) was well advanced, where growing in or around permanent ponds in the marsh. The wrens in these latter areas were generally paired at this time and, from all indications, nesting was well under way. In early May the new bulrushes were of sufficient height (three to four feet) to apparently encourage nesting on the part of the females, because solitary individuals in such patches became the exception rather than the rule, as was true the previous month. By the middle of the month, eggs and young were to be found. On May 18, 1938, two such areas, that in early April had contained only nest-building males, were examined. In one, a pair was found to have four eggs deposited in one of the several available nests. In another closely adjacent tract of bulrush another pair was found to have a nest containing five small, downy young.

The nests were composed of cat-tails, or bulrushes, for the most part, these largely being dead stems with a few of the new, green, growing stalks of the supporting plants woven in. The lining consisted of cat-tail down and feathers.

Toxostoma redivivum (Gambel)—California thrasher

Common resident; chaparral associations.

Thrashers were common on the dry inland ridges where manzanita, chamise, chinquapin, chaparral pea, bush poppy and scrub oak were dominant, as well as along the coast where chaparral broom, coffee berry and wild lilac comprised the principal cover. They were, likewise, quite common in sand

dune areas back of the coastal beaches where lupine and lizard-tail formed a fairly dense cover.

On April 30, 1936, a pair, believed to be nesting, was observed in a lupine-grown area at Franklin Point. One individual, thought to be the male, sang almost continually from the top of a bush until close approach was made. The other member of the pair was seemingly alarmed at the observer's presence and flew about the lupine patch in a distressed manner.

Turdus migratorius Linnaeus—Robin

Possible winter visitant.

Robins were seemingly rare in this region, being noted on only two occasions. On April 15, 1938, several individuals were seen and heard in a grove of Monterey pines about one-third of a mile south of the mouth of Waddell Creek and on March 15, 1939, a number were observed in open grassland near Butano Creek in Hidden Valley.

Ixoreus naevius (Gmelin)—Varied thrush

Winter visitant; forested areas.

This species was one of the most common avian species in the redwood-Douglas fir association during the winter months. Individuals were noted principally on the forest floor, in forest undergrowth and on the lower limbs of trees. This species was also fairly common in Douglas fir-forested areas. The latest date on which varied thrushes were noted was April 10, near Butano Falls.

Hylocichla guttata (Pallas)—Hermit thrush

Resident as well as winter visitant; forested regions.

Hermit thrushes were common residents of the redwood-Douglas fir association throughout the year, although their population was considerably augmented during the winter season by an influx of wintering individuals. At certain times numbers of individuals appeared to be just passing through. Thus, on the afternoon of March 4, 1936, in San Mateo County Memorial Park, large numbers of hermit thrushes were observed. In one instance, in the late afternoon on a brushy slope just above a redwood grove, the writer saw seven individuals pass beneath a single chaparral broom plant in the course of two minutes. Each bird was moving down the slope, independent of the other and occasionally pausing to forage for a moment or so.

Forested slopes appeared to be preferred to the floors of canyons where the redwood growth was extremely dense. The margins of forests, adjacent to brushland, were often selected by hermit thrushes during the nesting season.

Hylocichla ustulata (Nuttall)—Russet-backed thrush

Summer visitant; principally riparian association.

The earliest date on which members of this species were noted was April

16. Russet-backed thrushes were restricted in this region to the coastal portion, outside the redwood belt proper, where they occurred largely in riparian growth.

Sialia mexicana Swainson—Mexican bluebird

Resident, principally knob-cone pine association and grassland.

Mexican bluebirds were noted only in very open knob-cone pine areas in the eastern part of this region. Here much of their food was obtained by flying out from the upper parts of the trees after nearby insects in the air. Probably the berries of manzanita and other types of shrubs were also consumed. Along the coast, members of this species were found in or adjacent to open grassland where telephone lines, fences and the tops of various bushes were used as perches. On April 14, 1936, four miles east of Pescadero, a bluebird was seen to fly up from the ground to the top of a telephone pole with what appeared to be a worm in its bill.

Bluebirds were frequently seen along the ocean beach in the southern part of this region. Here they perched on driftwood or on the sand. Sometimes when in flight, particularly on windy days, they appeared to hover before alighting momentarily on the sand.

Corthylio calendula (Linnaeus)—Ruby-crowned kinglet

Winter visitant; oak-madrone association.

During the winter months ruby-crowned kinglets were very numerous in the live oaks, although they were frequently seen in other types of trees as well. The latest date on which members of this species were noted was April 8. By the middle of March, however, males could regularly be heard singing.

Anthus spinoletta (Linnaeus)—Pipit

Winter visitant; open land.

Pipits were seen irregularly during the winter months, occurring in the western portion of this region in situations similar to those occupied by horned larks. On November 3, 1938, a single bird of this species was observed bathing in a small rain puddle in the middle of a dirt road near Pescadero Point.

Bombycilla cedrorum Vieillot—Cedar waxwing

Irregular visitant.

Cedar waxwings were noted only once. On May 14, 1936, in the southwestern portion of the town of Pescadero, a group of these birds was noted during most of the morning in cottonwood trees along the creek. Individuals would regularly fly out from about fifteen to forty feet into the air, apparently after insects, and return to a different perch.

Lanius ludovicianus Linnaeus—Loggerhead shrike

Probably resident; open land.

Shrikes were seemingly scarce in this region, being noted on a few occasions

in open country near the mouth of Gazos Creek. In each instance of observation individuals were seen perched on telephone wires along roads adjacent to weedy fields.

Vireo huttoni Cassin—Hutton vireo

Common resident; oak-madrone association.

Hutton vireos were common, especially inland where they frequented live oaks and other woodland types of trees. They were sometimes noted in old logged-over areas, where second growth redwood and Douglas fir were mixed with rather arid chaparral species.

Members of this species were heard singing from the latter part of February to the end of June. On June 10, 1935, near Sky Meadow in the Big Basin, the writer was able to call a pair of Hutton vireos to within six feet of him by repeatedly whistling two of their call notes.

Vireo gilvus (Vieillot)—Warbling vireo

Summer visitant; woodland.

In the eastern portion of this region warbling vireos were fairly common in oak-madrone associations, where not too dry or where they were adjacent to redwood forest. Coastwise, members of this species showed a definite preference for deciduous trees, such as cottonwoods and willows growing along stream banks.

The earliest date of observation for this species was March 19.

Vermivora celata (Say)—Lutescent warbler

Summer visitant; oak-madrone association.

The earliest date on which lutescent warblers were noted was March 13, in San Mateo County Memorial Park. The males were heard singing almost from the time of their arrival, although it was not until the first part of April that pairs were noted. On June 24, 1935, on China Ridge, a female was seen carrying food in her bill. On March 20, 1936, in San Mateo County Park, a careful check was kept on one singing male for a period of five minutes. During this time it was heard to sing at intervals varying from eight to sixteen seconds. The average lapse of time between songs was thirteen seconds.

Members of this species were characteristic of the oak-madrone association, occurring occasionally in willows in canyons where tracts of chaparral or woodland were adjacent. The madrones, however, were most attractive to these birds and were frequented more than oaks and other woodland trees.

Dendroica aestiva (Gmelin)—Yellow warbler

Summer visitant; principally coastal riparian.

Yellow warblers were seen only in the western portion of this region where they frequented willows and cottonwoods growing close to streams.

Dendroica auduboni (Townsend)—Audubon warbler

Common winter visitant; mainly coastwise.

This species was observed between October 6 and April 10 throughout the entire area. Individuals were most numerous, however, in the western section where they were found in many diverse situations. Trees such as cottonwood and alder, which were leafless during the winter, were most frequented. Audubon warblers foraged over these trees and also used them as perches from which they would dart out after flying insects. Coniferous trees, brush, telephone wires, fences and even bare rocks along the ocean shore were also frequented.

In the latter part of March and in early April, before their exodus in migration, singing individuals were commonly heard.

Dendroica nigrescens (Townsend)—Black-throated gray warbler

Probably summer visitant.

On June 1, 1935, a black-throated gray warbler was seen and heard singing high up in a Douglas fir on Butano Ridge. It is likely that a few members of this species breed locally in the higher parts of this region.

Dendroica townsendi (Townsend)—Townsend warbler

Winter visitant; woodlands and Douglas fir forests.

Townsend warblers were present in moderate numbers in this region until April. They were found most frequently in live oaks and Douglas firs growing apart from dense stands of redwoods. Occasionally, they were noted in cottonwoods along the coast. Individuals were regularly heard singing after the middle of March. Prior to this time the only note that Townsend warblers were heard giving was a single "pit," usually given after long intervals of silent foraging. When foraging, members of this species were seen principally about the terminal twigs of larger trees.

Dendroica occidentalis (Townsend)—Hermit warbler

Possible resident in small numbers.

McLean (Condor, 38, 1936, p. 17) recorded the taking of an adult male "in full breeding condition" on June 10, 1933, three miles north of the La Honda summit of the Santa Cruz Mountains, in San Mateo County. On June 11, 1935, at mid-morning, the writer heard a warbler of questionable species singing high up in a Douglas fir on the western slope of the ridge separating the East and West Forks of Waddell Creek. Believing it to be a black-throated gray warbler, which species had been noted ten days previously several miles from here, about forty-five minutes were unsuccessfully spent in trying to see the individual. On returning about one hour later to the same locality the singing individual was no longer heard, so an attempt was made to locate it by "squeaking." After first attracting chestnut-backed chickadees, juncos and western flycatchers, a female hermit warbler was seen inves-

tigating the source of disturbance. The bird came within about six feet of the observer. This locality is about twelve miles south of where McLean (*supra cit.*) collected a hermit warbler.

Geothlypis trichas (Linnaeus)—Yellow-throat

Resident in moderate numbers; marshland or bordering marsh land.

Yellow-throats were noted around Pescadero Marsh, the marshes at the mouths of the Arroyo de los Frijoles and Waddell Creek and about swampy places in the sand dunes on Franklin Point. Individuals of this species, while observed principally in cat-tails and tules, were also seen to frequent brush, such as lupine and lizard-tail, bordering marshy places. Yellow-throats were heard singing from April to July. On May 18, 1938, in Pescadero Marsh, a pair was seen to become quite alarmed when the observer approached close to a clump of bulrushes in which they were located. Judging from their behavior they had a nest nearby.

Wilsonia pusilla (Wilson)—Pileolated warbler

Summer visitant; forest and woodland.

The pileolated warbler was found to be a rather typical inhabitant of the redwood-Douglas fir association, not being restricted, however, to this habitat. Members of this species very often frequented oak-madrone woodlands and riparian growths of alder and willow, both inland and along the coast. In forested areas pileolated warblers were found to occur principally around small clearing or in situations, usually rather sunny, where tan oaks or madrones were growing. Large wild lilac bushes growing along the margins of forests, were especially attractive to these warblers. On several occasions individuals were seen foraging in bracken.

On the morning of May 23, 1935, about one-quarter of a mile south of Sky Meadow, four male warblers of this species were observed singing, at times within fifty feet of each other, in a rather dense oak-madrone woodland. Each appeared to be trying to defend territory against the other three and each made unsuccessful attempts to drive the others away. On Waddell Ridge on July 9, 1935, a male was seen carrying food in his bill.

The earliest date on which members of this species were noted was March 18.

Passer domesticus (Linnaeus)—English sparrow

Introduced resident; immediate vicinity of human habitations

English sparrows were common about the town of Pescadero and were noted about the buildings of several of the larger farms along the coast highway. On April 17, 1935, a practically completed nest belonging to a pair of this species was noted beneath the eaves of a house in Pescadero.

Sturnella neglecta Audubon—Western meadowlark

Common resident; grassland.

Meadow larks occur commonly in the western part of this area, frequenting meadow and pasture land, as well as grassy hillsides. Unlike horned larks, which occurred in the same general open grassland, members of this species were generally observed to avoid cultivated fields.

Agelaius phoeniceus (Linnaeus)—Red-winged blackbird

Resident, increasing in numbers during winter season; marshes and moist meadow land.

Red-winged blackbirds were present in many localities along the coastal part of this region. Although they occurred in greatest numbers in Pescadero Marsh, they were also found about the small marshes near the mouths of several of the other creeks, around reservoirs where tules or cat-tails were growing and in meadows and pastures wherever there was sufficient moisture to produce a rank growth of weeds and sedges. Where inhabiting the last-mentioned type of situation a definite preference was shown for the vicinity of roads and fences. Telephone poles and wires as well as fences were used as perches and singing posts.

Redwings were present in greater numbers in the winter than during the summer season, this increase in population probably resulting from the arrival of wintering individuals of other races. Greatest numbers, however, were observed in April, whereas in May the numbers were much reduced. Nesting activities extended from the middle of April to the end of June. On June 25, 1935, two pairs were seen carrying food to young in nests located in a patch of cat-tail about forty by fifty yards in size, growing close to a reservoir one-quarter of a mile east of the mouth of White House Creek.

Euphagus cyanocephalus (Wagler)—Brewer blackbird

Common resident; coastwise.

Brewer blackbirds were noted commonly about the town of Pescadero, where individuals were seen on lawns, streets, perched on telephone wires and in cultivated trees. They were also observed about the mouths of creeks, such as Gazos and White House and near meadow land. Flocks were noted up to the latter part of March, but by the middle of April nesting activities were well under way. Very large flocks of Brewer blackbirds were seen in the fall of the year. On October 22, 1937, two flocks, each estimated to consist of approximately one thousand individuals, were seen within the limits of the town of Pescadero and additional smaller aggregations were observed flying over the nearby marsh.

Hedymeles melanocephalus (Swainson)—Black-headed grosbeak

Summer visitant; principally woodland.

Black-headed grosbeaks were moderately common in oak-madrone woodlands throughout this region, occasionally frequenting Douglas firs. Along the coast they often inhabited willows, cottonwoods and alders. The earliest date on which this species was noted was April 23.

Carpodacus purpureus (Gmelin)—Purple finch

Common resident; knob-cone pine, also to some extent Douglass fir association.

Purple finches were observed in Douglas fir forests and in woodland, but by far the greater number seen were associated with knob-cone pines. As a consequence, the purple finch populations centered on the rather barren chaparral- and pine-covered ridges. During May, 1935, the availability of certain types of food appeared to be a critical factor governing the distribution of members of this species. Large numbers of finches were observed on China Ridge, feeding on the berries of *Arctostaphylos tomentosa*. On the adjacent Waddell Ridge, where knob-cone pines were equally abundant but *Arctostaphylos tomentosa* was largely replaced by *Arctostaphylos sensitiva*, purple finches were extremely rare. This last mentioned species of manzanita was just in flower and, consequently, failed to provide suitable food.

Singing individuals were heard from the end of February until July. On June 6, 1935, on China Ridge, an adult male purple finch was seen displaying on a rock before a female, perched a few feet away on a yerba santa bush. The male sang and extended his wings which were vibrated rapidly. At the same time he kept turning around.

Carpodacus mexicanus (Müller)—Linnet

Common resident; principally near the coast.

Linnetts were widely distributed throughout the year in the western part of this area, occurring about buildings, in moderately open brushland and woodland, weedy meadow land and sand dune. They were observed in large flocks in the autumn, sometimes over two hundred individuals comprising one aggregation. Later in the year, and in the early spring, the flocks appeared to be smaller. On January 26, 1938, after observing a number of flocks of linnetts, it was apparent that the males frequently congregated by themselves.

During the nesting season the species was most abundant about coastal brush, especially on the tops of bluffs, just back of the ocean beach, and on brush-covered sand dunes. On Franklin Point, on the early morning of April 30, 1936, a pair of linnetts was observed perched on the top part of a willow tree which was about seven feet high and surrounded by chaparral broom and lupine growing on sand dunes. When a close approach was made the birds reluctantly flew a short distance away. On investigation a nest was found a short ways below where they had perched, at a height of five feet. The nest was on the western side of the tree and was composed of grass stems, rootlets and plant fibres. It was nearly complete except for the cup. Some fresh rootlets, recently taken from living plants, were lying on twigs close to the nest. While the writer was observing the nest the pair came within four feet of him.

Spinus pinus (Wilson)—Pine siskin

Fairly common resident; usually in the vicinity of forest land.

Pine siskins, while noted principally about coniferous growth, were often

seen to forage some distance away from trees. During May, many flocks obtained much of their food from manzanita (*Arctostaphylos tomentosa*) berries which matured early on the warm chaparral-covered slopes. Later in the summer, bull thistle (*Cirsium lanceolatum*), often found along roadsides, formed an important item of food. On February 26, 1936, while walking beneath a group of tall redwoods in San Mateo County Park, a noise resembling falling rain drops was heard in the relatively quiet forest. The rain drops proved to be redwood seeds. Careful investigation of the trees above revealed a flock of about sixty pine siskins feeding on the redwood cones. They were not heard to utter a sound during the ten minute period of observation, although they were distributed over the tops of several trees. The only indications of their presence were the falling seeds and occasional movements on the part of the individual birds that were visible from below.

On June 17, 1935, near Cliff Caves, about one mile northwest of the Big Basin, a flock of pine siskins was seen on a bare sandstone outcropping in the chaparral. On closer approach the birds appeared to be rubbing their bills on the rock.

Spinus tristis (Linnaeus)—American goldfinch

Common resident, locally; coastal riparian, brush and weed-grown areas.

American goldfinches were seen only in the western parts of this region where they most commonly were associated with cottonwoods, alders and willows growing along creeks, and in coastal brush, such as lupine, chaparral broom and wild lilac. Much of their food was derived from weed-grown fields and weed patches along road sides. In the early spring, alfalfa (*Erodium*) and mustard seeds constituted very important items of food for goldfinches. Later in the season, and during the summer, the seeds of sow thistle (*Sonchus asper*) and bull thistle (*Cirsium lanceolatum*) were sought after intensively. In 1936, signs of breeding activity were noted early in April, when singing males were observed in cottonwood trees along Pescadero Creek. Males were often seen chasing each other and pairs were of common occurrence. On April 17, the female of one pair was observed gathering small fragments of cotton, apparently for nesting material. On May 15 of this year a female was seen carrying nesting material.

Flocks were observed during the entire year, even in the nesting season. On May 18, 1938, flocks composed of thirty or more individuals were noted, although many nesting pairs were seen on this date.

Spinus psaltria (Say)—Green-backed goldfinch

Resident, but not numerous; coastwise.

Although probably resident in small numbers in chaparral and grassland parts of this area green-backed goldfinches were observed only once, near the mouth of Gazos Creek. The apparent scarcity of this species seemed strange in view of the abundance of pine siskins and American goldfinches.

Pipilo maculatus Swainson—Spotted towhee

Common resident; chaparral.

Spotted towhees were common in brushland throughout the entire area. They frequently were observed in oak-madrone woodlands where there was an abundance of undergrowth, also in burned-over areas where new, low second-growth redwood and Douglas fir were mixed with wild lilac and certain other species of brush. In 1936, it was not until the end of the first week in April that territorial song was heard. On July 10, 1935, an individual was seen carrying food in its bill near Hollow Tree Camp at the head of the East Fork of Waddell Creek. Apparently this species nests late in this region.

Pipilo fuscus Swainson—Brown towhee

Resident, locally; brushland.

The distribution (more properly, absence) of brown towhees over most of this region proved very puzzling. Immediately north of the town of Pescadero brown towhees were found to be numerous in the coastal brush. A few were noted about Pescadero and individuals were occasionally seen on a brushy hill one-half mile southwest of here. The only other locality along the coast, within the area studied, where brown towhees were observed was in the immediate vicinity of a farm, situated along the coast highway, one mile northwest of the mouth of Waddell Creek. Three miles southeast of the mouth of Waddell Creek, outside of the boundary of the area in which observations were made, brown towhees were numerous. No reasonable explanation can be offered for their absence over this ten-mile strip of territory along the coast between the two points at which they were observed, as there is no geographic barrier present and little perceptible difference in vegetation. It is possible a few brown towhees may be present in this region but, if so, they are very scarce as repeated attempts by the writer to locate any were without success. Brown towhees were noted in the eastern part of this area only near Blooms Mill, at the southeastern entrance to California Redwood State Park.

Passerculus sandwichensis (Gmelin)—Savannah sparrow

Resident and winter visitant; grassland and marsh.

Savannah sparrows were present throughout the year in the western part of this area, their numbers being considerably augmented, however, during the winter by the arrival of migrants. Members of this species frequented open meadow land, small grassy patches present in many places on the tops of bluffs back of the beaches, and marsh flats where salt grass, pickle-weed and silver-weed were growing.

By the first part of March, in this region, most of the wintering Savannah sparrows had left and the resident birds were paired. On May 12, 1936, in an open, grassy patch on top of a bluff, just south of the mouth of Pescadero Creek, a nest of this species was found after the pair was seen to fly several times to approximately the same spot. Four young, about two days old, were found in the nest. Their eyes were, as yet, unopened. The nest was on the

ground at the base of a clump of fox-tail grass and was composed of fine grass stems. One of the parents, thought to be the female, was with the young when they were found. When the observer came within one foot of her she fluttered off the nest and along the ground, feigning injury to attract attention. The male frequently sang from the top of a dead stalk, about eighteen inches in height, which was located twenty feet away. On May 15, when the nest was examined, the young were partly feathered and had their eyes partly open.

On April 2, 1938, at the same location where the nesting pair was observed two years previous, a pair of Savannah sparrows was seen. From their behavior it was thought that the female might be laying. The male was observed singing regularly from a low perch. The female foraged in the grass most of the time. Once the pair was seen to copulate on the ground, after which the male flew to his singing post thirty feet away. The observer was unable to find a nest when a hasty search was made, but the pair exhibited much alarm during this time. On April 15, 1938, when opportunity was next afforded to make observations in this area, only the male was seen. He regularly sang from several singing posts within the same territory where the pair was noted thirteen days previously. Between songs he spent most of the time foraging. It appeared as though the female was incubating as the male became alarmed when the observer approached the territory.

Males were heard singing on August 15, 1937, along the coast just south of Pescadero Creek.

Junco oregonus (Townsend)—Oregon junco

Resident and winter visitant; woodland and forest.

Juncos were commonly associated with redwood forests and woodlands, usually near redwood forests. In the winter, when many non-resident flocks were present, oak-madrone woodlands were frequented to a greater extent. Resident juncos were paired by the end of the first part of March, even though the flocks of winter visitants did not leave until a month or so later.

In the middle of the afternoon of May 29, 1935, a pair of juncos was observed feeding a young individual near Sky Meadow. The young was concealed in a small clump of ferns near a live oak at the edge of a slight clearing. Whenever the female would return to the vicinity the male would fly to a low dead limb of a wild lilac bush, about twenty feet away, and turn about rapidly, displaying the white tail feathers. After the female had fed the young the male would either fly away with her or go to the top of a nearby tree and sing. This behavior was observed repeatedly. On two occasions a Stellar jay was seen to search about in the vicinity of where the female usually disappeared in the grass. It appeared each time as though the jay was searching for the nest or young. This disturbed the juncos very much and caused them to constantly give warning "thups" and make effort to distract the jay. They became similarly alarmed and called and displayed when the observer came close to the young, which was able to fly a few feet.

Many immature juncos were seen during the second week of June in 1935.

Spizella passerina (Bechstein)—Chipping sparrow

Summer visitant locally.

Chipping sparrows were only observed in the easternmost part of this region, near grassland. They were noted near Sky Meadow and in trees on the margins of open, grassy hillsides, about one-half mile northeast of Sky Meadow.

Zonotrichia leucophrys (Forster)—White-crowned sparrow

Resident and probably winter visitant; principally coastal brush.

White-crowned sparrows were commonly seen in the western portion of this region in coastal chaparral, composed largely of chaparral broom and poison oak. Close to the ocean they were seen to frequent lizard-tail and lupine bushes.

During the fall and winter many flocks were seen, probably a certain number of them being composed, at least in part, of non-resident birds. Song was heard occasionally during this period, but it was not until the first part of March that singing individuals were heard in numbers. On April 30, 1936, a white-crowned sparrow was noted carrying nesting material to a lupine-covered area on Franklin Point. On May 7, 1936, just south of the mouth of Pescadero Creek, a pair of white-crowned sparrows was seen building a nest in a lizard-tail bush, situated on the side of a bank. Only a platform of grass stems had been constructed at this time, at a height of three feet above the bottom of the bank.

Zonotrichia coronata (Pallas)—Golden-crowned sparrow

Winter visitant; brushland, principally coastwise.

Golden-crowned sparrows occurred in winter over most of the chaparral-covered areas, but were most numerous along the coast particularly in brush bordering creeks, in lupine along the bluffs and on sand dunes.

Melospiza melodia (Wilson)—Song sparrow

Resident and probably winter visitant; brush and dense herbaceous growth.

Members of this species were absent from the dry chaparral and extensive redwood tracts but were present in numerous other habitats. Riparian brush, outside of dense forest or woodland cover, brush and woody patches about springs and seepages, coastal chaparral, marsh growth, cultivated shrubs and other similar types of cover were frequented. Resident birds were heard singing frequently by the end of January and, judging from the alarm exhibited by pairs when the observer encroached upon their territory, nesting activities were well under way by the end of February. Indications of nesting were observed up to the first part of June.

Populations and Habits of the Fox Squirrel in Allegan County, Michigan

Durward L. Allen

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Among southern Michigan upland game the western fox squirrel, *Sciurus niger rufiventer* (Geoffroy), is exceeded in importance only by the pheasant and the rabbit. Kill records for this species were first available in the 1939 season, and tabulations indicate that approximately 619,000 fox squirrels were killed by 541,000 small game hunters in that year.

The state was closed to the hunting of squirrels during 1938 as a result of an unexpected action of the 1937 legislature. Reports following the enactment of this measure indicated that the fox squirrel was plentiful over much of its range within the state, and this divergence of opinion focused attention upon population levels and management of the species. Accordingly, from September 1937 to December 1939, in such time as could be spared from other duties, I conducted an investigation of fox squirrel numbers and habits.

The ultimate objective of this study, as with all of the Game Division research program, is more game through habitat improvement. During the investigation this goal was kept constantly in mind. The empirical method of testing habitat alterations on experimental quadrats requires intensive and continuous study. Neither time nor equipment was available for that type of research during the two years of this work. However, as the scanty literature amply attests, little is known of the biology of squirrels—their numbers, fecundity, or mortality factors. It is this fundamental knowledge that makes possible an intelligent approach to management. Hence the present work is preliminary in nature, intended to contribute toward information on the adjustment of fox squirrel populations to one type of environmental complex.

This inquiry was made at the Swan Creek Wildlife Experiment Station in Allegan County during the first two years of that institution's existence. From August to November 1937 I lived at a W. P. A. camp near the station; from the latter date until July 1938 my residence was in Allegan, ten miles from the study area. In July the headquarters at the station became available and the remainder of the work was carried on from there.

From the standpoint of the squirrel investigation, it was fortunate that Arnold O. Haugen began his rabbit research at the experiment station in January 1938. Haugen used the same kind of traps and the same bait that were used for squirrels. As a result many squirrels were taken in the rabbit traps and good records secured. Without Haugen's cooperation the data given here would be considerably less complete than they are. I wish also to acknowledge the records contributed by F. W. Stuewer, whose extensive raccoon trap-line took many fox squirrels: As these traps were set in the riverbottom they gave a sampling in a different type of habitat from the upland studies. In addition, I am indebted to Philip S. Baumgras, Robert C. Dunning, and Merrel A. Taylor, who ran traps and otherwise assisted in the work during the two summers.

History of the Fox Squirrel in Michigan

According to Kennicott (1856), the fox squirrel was originally a creature of the prairie edge. In Illinois and Wisconsin, oak groves occupied the ridges in the prairie and formed the westernmost outposts of the forest land. In northern Indiana and the southwestern counties of Michigan the land was for the most part wooded, with here and there patches of sod that formed the "oak openings" or eastern vestiges of the prairie. This was the typical primitive habitat of the fox squirrel.

Over most of Michigan and Indiana the dense deciduous forest was occupied by the gray squirrel. At the time of settlement of this state the latter species was abundant, and the fox squirrel was found only in the more open growth of the southern counties (Wood 1922). The gray squirrel largely disappeared with the cutting of the heavy timber; and with the creation of a pseudo-prairie-edge condition on the partly cleared farms, the fox squirrel rapidly extended its range.

Evermann and Clark (1911) stated that the fox squirrel was appearing in the Lake Maxinkuckee region of Indiana in 1900. In 1907 Hahn (1907) found the species occupying the upland and lowland woods of the Kankakee Valley. In 1908 the same author (1908) found fox squirrels common in the smaller open growth of the farmland around Mitchell, Indiana, but he stated that gray squirrels inhabited the large deciduous timber. McAtee (1907) reported a similar condition in Monroe County, Indiana.

In Michigan, Norman A. Wood (1922) observed the first fox squirrels at his home in Lodi Township, Washtenaw County, in about 1875, and they were rare for several years after that. Gray squirrels were still so plentiful in

Osceola County about 1900 that O. J. Wenzel (1912) reported it not uncommon for a hunter to kill 10 to 20 in a day. By 1912, however, the species was nearly exterminated in that region and was being rapidly replaced by the fox squirrel in the remaining woodland. By 1922 the fox squirrel had spread as far north as Charlevoix County, near the northern tip of the lower peninsula, the first record being reported in the winter of 1922-23 by J. H. Stephenson (Dice 1925).

At present the gray squirrel is abundant only in the northwestern portion of the lower peninsula, where it persists in hardwood timber. The fox squirrel now occurs in every part of the lower peninsula, although it is less plentiful in the northern counties. Hunters' kill reports indicate that approximately 18,900 fox squirrels were killed in Allegan County in the 1939 open season. This was exceeded by four other counties.

The Area

At a time when glacial ice was still keeled into the Lake Michigan basin, Lake Chicago extended between moraines northward into the center of Allegan County. In water that was approximately 60 feet above the present level of Lake Michigan a deep layer of fine sand was laid down. This deposit, termed "Plainfield sand" (J. O. Veatch, personal communication), forms the major soil type in a roughly square area of marginal to submarginal land about 100,000 acres in extent.

Within recent times this tract was occupied by a white pine forest which, due to the sterility of the soil, was only partially invaded by oak. Thus an "island" of pine was left in the deciduous forests of southwestern Michigan. A century ago settlers were moving into Allegan County, and in the ensuing fifty years most of the pine was lumbered off. Fires swept the area and destroyed much of the thin layer of humus that had accumulated on the forest floor. Numerous homesteads were established on the cleared land, but it was ill-suited to farming. After a few mediocre crops the soil was impoverished, and the would-be farmers with it.

White pine in the upland was succeeded by a second-growth of poplar (*Populus grandidentata*), sassafras (*Sassafras variifolium*), and black and white oaks (*Quercus velutina* and *Q. alba*). At present the oaks are dominant, with individual pines or small groves scattered over the area. In this growth flowering dogwood (*Cornus florida*) is the most important secondary species.

The Kalamazoo River cuts diagonally across this area in a floodplain divided by numerous bayous. The latter are fed by springs flowing out of the high bank which rises abruptly 40 to 60 feet to the upland. Swan Creek joins the river in a similar valley at the experiment station headquarters.

The stream bottoms support extensive lowland woods consisting principally of American elm (*Ulmus americana*), red maple (*Acer rubrum*), and white and black ash (*Fraxinus americana* and *F. nigra*). Between the moist flood-

plain of the bottoms and the sandy upland a narrow strip of mesophytic soil lies on the steep slope of the escarpment. This condition is made evident by the beech trees (*Fagus grandifolia*) which grow on the side of the acclivity and practically nowhere else. Along the bank there are also occasional clumps of hemlock (*Tsuga canadensis*). The few gray squirrels inhabiting the region appear to be associated with this habitat. They are not infrequently seen in the bottoms, but seldom venture far into the oak upland.

In 1935 the U. S. Department of Agriculture, in its resettlement program, began to purchase land in this area. About 35,000 acres were acquired and various developments carried out. In 1940 the State of Michigan assumed administration of the tract, under a long-term lease, as a wildlife experiment station and state forest.

Figure 1 shows the present character of the area and the relative continuity of the woodland. It is notable that this upland supports black and white oaks, but not the red oak and hickory commonly found on better soils. The absence of hickory appears to result in a lower squirrel population than in farmland timber. In certain deserted fields wind erosion has been extensive, and acres of blow-sand impart a dune-like appearance of aridity not belied by the widespread occurrence of the prickly pear cactus (*Opuntia rafinesquii*) and occasional stalks of yucca (*Yucca glauca*).

Methods

Most of the data in this report were obtained by live-trapping, ear-tagging, climbing trees for nest examinations, making autopsies of dead animals, and tracking in the snow. A total of 728 individual fox squirrels were handled either alive or dead. Of this number 660 were taken in box traps 1,101 times. Laboratory examinations were made on 283 dead animals.

The traps used (Fig. 2) were one foot square in cross section, two feet long, and were covered with $\frac{1}{2}$ -inch-mesh, 16-gauge, galvanized hardware cloth. They were baited with an ear of corn and a piece of dried herring. The corn served to attract squirrels and rabbits, and the fish was for raccoons, opossums, skunks, and house cats. Most of the traps at the station were baited with this combination for the benefit of the various studies in progress.

In my own squirrel work I handle the animals with a pair of horsehide mittens. The trap is set on end and the sliding door opened enough to allow the operator's arm to be inserted to the shoulder. The squirrel is then seized with a firm grip on the back of its neck. The mitten is necessary, as a squirrel's hind feet and claws can do serious damage. In emergencies, when a mitten is lacking, it is best to grasp the base of the animal's tail and pull backward. The squirrel will dig in and resist. With his free hand the operator can quickly grasp the back of its neck, with plenty of downward pressure, and stretch the squirrel out to prevent scratching.

The use of a mitten is simple, but requires practice, and a better method was evolved by Stuewer. He handled raccoons in a cone of inch-mesh poultry

netting and found that it worked equally well for squirrels. Other members of the staff adopted it with entire success.

At the Kellogg Farm (Allen 1938) I marked squirrels by toe-clipping and ear-notching. In the Allegan studies the animals were marked with ear tags—males in the right ear and females in the left. This method has the advantage that it can be seen at a distance and that hunters will notice and return the tags. It has the disadvantage that some animals tear out the tags. Young squirrels in the nest were toe-clipped.

At the experiment station each trapline had a number and each trap was numbered within the line. In trapline operation the daily catch for each trap was recorded on a 5" x 8" form printed for the purpose. A captured animal was weighed on a spring field scale accurate to about 1/2 ounce. It was also sexed and examined for signs of breeding, lactation, parasites, disease, and general condition. Notes were taken by a system of symbols on the trapline record, and later in the office transferred to a 4" x 6" card which contained the history of the individual. Dead squirrels were autopsied and the information recorded on another 4" x 6" form used in the station catalog.

Populations

In the fall of 1937 an area was selected for population studies. The particular quadrat was chosen because it was fairly well separated from the surrounding woods and because the size of the stand appeared to be about the average of the second-growth oak woodland. Superficially it seemed that the squirrel population in this tract would be as representative of the oak upland as any that could be chosen. Enough cutting was done to separate the unit from woodland adjoining to the northeast and to trim it to 40 acres. Locations for 36 traps were established in a checkerboard pattern. This divided the woods into 36 smaller plots of slightly more than an acre each which were numbered like the sections in a township. The "squirrel woods," as it was familiarly known and will be designated here, is trapline number 1 in the Swan Creek series.

HABITAT DESCRIPTION

The woody vegetation in the squirrel woods was analyzed quantitatively. A total enumeration was taken of the woody plants above 3 feet in height on 36 chain-square plots, or an 8.86 percent sample of the woods. Figure 3 shows the character of the stand.

The analysis showed that 89 percent of all trees over 10 inches in diameter at breast height were black oaks; five percent were white oak and 5 percent white pine. In the 3- to 10-inch class, white oak formed 75 percent, black oak 20 percent, and white pine 2 percent. In the 1- to 3-inch group, white oak totaled 81 percent of the woods, with black oak, white pine, and black cherry (*Prunus serotina*) each forming between 1 and 2 percent. Flowering dogwood, which was the most important species in the understory, composed 13 percent of this class. Plants from 3 feet high to 1 inch in diameter were classed as reproduction; and flowering dogwood, sassafras, and white oak were found



Fig. 1. Aerial view of the Allegan "sand plains" and the course of the Kalamazoo River. The large lake was created by a power dam. The squirrel study woods is indicated by the arrow at lower left. Numbers are for sections in Valley Township, Allegan County.

to be most important with percentages of 41, 22, and 25 respectively. The remainder was made up of species of little significance.

The woods contains many old stumps which show that much of it was at one time nearly a pure stand of pines from 1 to 3 feet in diameter. Large numbers of trees were cut and left lying by the stump. It is apparent that many were badly fire scarred, which may be the explanation for the waste. Most of the logs and stumps are so rotted now that they can easily be kicked apart.

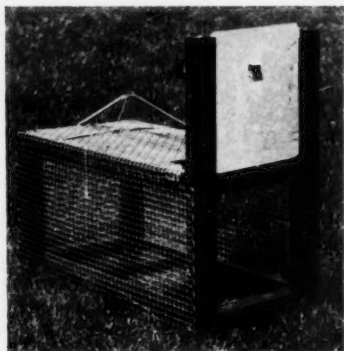


Fig. 2. The box trap used in the squirrel study. It is one foot square, two feet long, and covered with $\frac{1}{2}$ -inch mesh, 16-gauge, galvanized hardware cloth. Its principal disadvantage is that animals are exposed to weather. For squirrels alone the trap used by Baumgartner (1940) in Ohio is doubtless better.

It appears that, following the cutting of the pine, this area was taken over principally by black oaks. These are now being replaced by an active invasion of white oaks. This is indicated not only by the abundance of white and scarcity of black oak reproduction, but by numerous dead black oaks of various sizes scattered through the stand.

The ground cover in the woods is formed by clumps of huckleberry (*Gaylussacia bacchata*) and blueberry (*Vaccinium vacillans*), with wintergreen (*Gaultheria procumbens*) fairly evenly distributed. A small amount of greenbrier (*Smilax hispida*), rose (*Rosa* sp.), and pipsissewa (*Chimaphila umbellata*) is also to be found. It will be noted that several of these plants are much more common in northern than in southern Michigan forest land.

The woodmouse (*Peromyscus leucopus noveboracensis*) is the most numerous mammal in the woods. It is at home in the tree-tops and not infrequently inhabits old fox squirrel nests. A few rabbits and short-tailed shrews (*Blarina brevicauda talpoides*) occur there also, and the woods is visited by skunks, foxes, raccoons, badgers, and deer. The winter birds include the tufted titmouse, white-breasted nuthatch, chickadee, bluejay, red-bellied woodpecker, great horned owl, Cooper hawk, and crow. In summer the red-tailed and red-shouldered hawks are plentiful in the vicinity, as are the usual songbirds such as the red-eyed vireo, crested flycatcher, and Baltimore oriole.

SEASONAL NUMBERS

Trapline 1 was operated in nine periods during the two years of this work. Table 1 gives the dates of each period and summarizes the catch. Trapping periods in the quadrat are represented graphically in Fig. 4. These results indicate that during most of the year the number of squirrels using the woods was about 12, with a high in late fall (19 and 24) and a low in January (6 and 7). The populations in 1938 and 1939 appear to be comparable, with a small increase in 1939 after the closed season. There are complications, however, which cast some doubt on the authenticity of trapping figures as a census.

By tracing the history of individuals it was found that three squirrels each skipped a trapping period and then were caught again. Two more skipped a period twice and then were retaken each time. Two animals did not appear for two consecutive periods and then were caught. One squirrel was not trapped for three consecutive periods and then appeared in a trap. From these cases it might be inferred that the trapping did not in every period account for all resident animals. This is also implied in the radical fluctuation in the sex ratio as shown in Table 1. If we knew that each of the animals skipping one or more trapping periods was in the woods during the intervening time, these could be added to the known population. This is possible but by no means certain.



Fig. 3. The southeast corner of the squirrel woods in May. The oaks are just leafing out and dogwood is blooming in the foreground. A white pine can be seen at lower right.

TABLE 1.—Catch Summary for Trapline Number 1.

Trapping period	Males	Females	Individuals	Repeats
October 1937	4	8	12	7
January 20—February 11, 1938	3	3	6	20
July 30—August 22, 1938	9	3	12	20
December 7—December 27, 1938	7	12	19	12
January 11—January 20, 1939	3	4	7	7
February 16—March 7, 1939	5	7	12	15
March 23—April 12, 1939	9	3	12	13
June 26—September 3, 1939	3	7	10	8
September 30—November 24, 1939	13	11	24	52

Tending to counterbalance residents not caught are invading non-resident squirrels. Animals habitually using certain nests in this woods were considered residents, and all others non-residents. The population quadrat lies adjacent to other woodland at the northwest corner and along the northeast side (Fig. 1). It was particularly noticeable that outside animals entered the woods from these two directions.

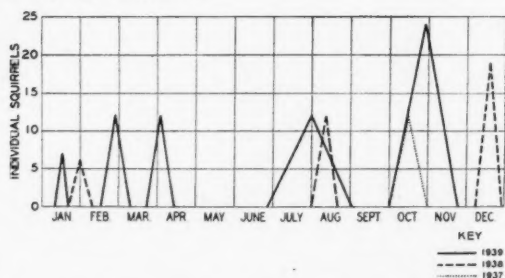


Fig. 4. A figurative representation of the squirrel woods trapping by periods from 1937 through 1939. Each trapping period is here shown as an inverted V, the distance between the legs indicating the length of the period and height of the apex the number of individual squirrels handled.

In December 1938 it was discovered that when a squirrel was liberated from a trap on snow it could often be trailed directly to a nest. Thus the trail of a non-resident usually led out of the tract to a nest elsewhere. When conditions were not suitable for tracking I usually followed the animal at a run, endeavoring to keep it in sight but not pressing it so closely as to make it tree. If a squirrel did tree, it sometimes kept on toward its nest by leaping from one limb to another. Usually, however, it merely crouched in a fork and waited. This was nearly always the case with non-residents far from "home." Several times a dog that would trail squirrels was available. This was found to be the best method of locating nests of individuals, as it was not dependent upon snow.

The breeding season population of the woods in 1939 was, if the total catch figures are used, 7, 12, and 12 respectively for the three periods early in the year. However, in the first period there is known to be 1, and probably 2, non-residents included. In the second there are 2, and in the third 3. It is

possible that not all non-residents were detected, as a dog for trailing was available on but few occasions. Hence it appears that the known resident squirrels in the tract numbered nearer 8 or 10 than the catch figure of 12.

Of the 19 individuals taken in December 1938 eight were never recaptured. Three of these were old animals and five were young of the year. Of the five young a male and a female were determined to be residents by locating their nests. Of the other three juvenile females probably all were non-residents, although only one was definitely established as such. Thus it appears that only about a dozen animals were certain residents of the woods, and that the large late fall catch indicates an increased movement of squirrels at this season. Possibly some young of the year are distributing themselves, or the apparent greater activity may be correlated with the harvesting of the mast crop.

The small catch of October 1937 is probably due at least in part to faulty technique. The trapping was not intensive, being carried out with only a dozen traps shifted around the edge of the woods. The quadrat was not laid out systematically until January. Under these conditions it is probable that not all of the squirrels present were handled. It is interesting to note that the catch of 6 in the following January compares closely with that of 7 a year later even though a kill of six squirrels was taken from the woods in the fall of 1937 and the entire region was closed to hunting in 1938.

Another complication to the population figures is that of lost tags. In the 40-acre quadrat squirrels repeated 154 times and lost 12 tags. Probably about half this number of animals were involved. Only certain individuals kicked at the ear tags, and one squirrel is known with fair certainty to have lost three. These errors were handled by judgment of individual cases.

It is somewhat disconcerting, after two years of fairly intensive trapping in an area as small as 40 acres, to find that I can not state precisely how many squirrels were resident at any one time. However, these figures for the squirrel woods, abetted by general observations, provide the basis for an estimate of population density that I believe to be sufficiently accurate for practical purposes. My judgment is that during the first year of this work the second-growth oak woods of the Allegan "sand plains" supported a late winter population of near one squirrel to 5 or 6 acres and a fall population of an animal per 3 or 4 acres. In 1939 the population density was somewhat greater than this, as will be shown.

COMPARATIVE POPULATION DENSITY IN 1938 AND 1939

The squirrel woods is a relatively small unit, and it probably is not wise to draw too many conclusions from work done on such a restricted area. As was pointed out, extensive traplines at the station were operated by Arnold O. Haugen and F. W. Stuewer in their respective studies of the cottontail and raccoon. Not all of these traps were in the same locations during both years of the work, and the amount of trapping was greater in 1939. But there

is no reason to believe that a rough comparison of the two years is not justifiable. The traps were scattered, singly or in quadrats, over more than five miles of stream and riverbottom, upland woods, and fields. Trap mortalities, as well as the variation in the amount and size of the woodland in the rabbit and raccoon traplines, make them of little use in calculating the population of squirrels on an acre basis. But by using trap-days as the unit of measurement it is possible to compare the relative population density of squirrels by calculating the percentage of traps which caught animals in the same periods during both years.

These figures were summarized by quarters beginning with January and the resulting data are given in Table 2. For a clearer comparison the percentages of traps which caught squirrels (designated "catch percentage") are plotted in Fig. 5.

There was general agreement among field men on this area that fox squirrels appeared to be more plentiful in 1939 than in 1938. The increase was most conspicuous early in the year before the leaves came out. Squirrels were easier to see at that season, and the larger number of observations made general impressions more reliable, but there is good reason to believe that throughout the remainder of 1939 fox squirrels were more numerous than in the preceding year—possibly by 20 to 30 percent.

It is logical that, since no hunting season crop was taken in 1938, an unusually large number of squirrels survived into winter. The closed season is certainly to be considered as a factor causing or contributing to the higher population of 1939. However, further trapping and observations in 1940 by Robert D. Montgomery (1941), indicate that fox squirrels continued to increase. Gray and black squirrels, on which there is a permanent closed season in this area, also steadily increased over the three-year period. The probability is strong, therefore, that during this study Michigan fox squirrels were undergoing an increase dissociated, at least in part, from the 1938 closed season.

A study of Fig. 5 indicates that the comparison of catch percentages is complicated by factors not anticipated. The decline in the catch from spring to summer in 1939 is the opposite of what happened in 1938 and antithetical to what would be expected if squirrels were more numerous the second year. It is true, however, that the trend early and late in the two years was much the same.

This apparent anomaly is explainable in terms of the mast crop. In 1937 and again in 1938 the crop of acorns in the Allegan region was poor. In 1939 an excellent production of mast furnished an abundant food supply from midsummer on. It is not unlikely that squirrels preferred acorns to the ear corn with which the traps were baited. During late fall and winter the increased efficiency of the bait in catching squirrels is indicated for both years by the similar rise in catch percentage.

TABLE 2.—Percentage of Squirrel Catches in Traps Baited with Ear Corn 1938-1939

	<i>Jan.-Mar.</i>	<i>Apr.-June</i>	<i>July-Sept.</i>	<i>Oct.-Dec.</i>
1938				
Trap-days	2,662	2,981	7,286	5,134
Squirrel catches	48	27	96	98
Catch percentage	1.80	.91	1.32	1.90
1939				
Trap-days	6,763	10,117	26,431	10,806
Squirrel catches	189	186	233	175
Catch percentage	2.79	1.84	.84	1.61

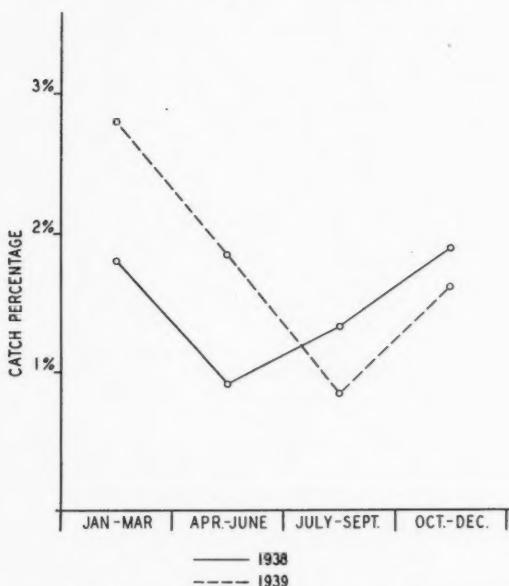


Fig. 5. A comparison, by quarters, of the percentages of box traps catching squirrels in the two years of the work. All traplines are included.

Nesting

In the Allegan area fox squirrels often inhabit second-growth devoid of tree hollows suitable for nesting. The squirrel woods contained four known tree cavities and only one was regularly used. Although leaf nests are sufficient for the survival of the species, hollows are probably preferred where satisfactory ones occur. This is inferred from the signs of long tenancy on certain old den trees (Fig. 6). The young are born and the animals pass the winter in either type of nest.

HOLLOW TREES

From my observations it appears that nearly any species of hollow tree may be used for nesting, provided the cavity is large enough and has a relatively small opening. The only large white oak in the population quadrat was hollow but was not used for nesting, for the apparent reason that the trunk was entirely open at the bottom. Elsewhere other trees in this condition were similarly avoided. On the other hand I found several trees hollow for most of their length, which had small entrance holes and which were dens of long standing. Although this probably illustrates the preference of squirrels it is not without exception. Stuewer has found young fox squirrels in hollows large enough for raccoons. On the banks of Swan Creek a black oak that was cracked apart had sticks wedged into place and a leaf nest built in the cavity. In another case a leaf nest was placed in the open top of a pine stub. In this study fox squirrels have been found living in white, black, and red oaks, American elm, large-tooth aspen, beech, white ash, sycamore, and red maple.

Knot holes and rotted crotches are favorite nesting places, and if the entrance is not large enough the animals gnaw it to the proper size. In live trees where the hole tends to heal this is usually between three and four inches in diameter. Baumgartner (1939) counted heal scars on a series of dens and found one hole which had been kept open by squirrels for at least nine years. There may be one or more entrance holes to a den.

There is one record from the population quadrat which indicates that particular animals become established and use a specific den for relatively long periods. A female, number 44415, was taken near the southwest corner of the woods in October 1937. The animal was probably a spring juvenile of that year. This squirrel was caught repeatedly in the same vicinity, and several times was tracked or followed to a red maple in a former farmyard at the edge of the woods. In 1939 she brought forth at least one, and probably two, litters of young in a hollow crotch of this tree. In December the squirrel was still there, and one or more of the summer young was using it at least occasionally. Although the red maple appeared to "belong" to the female in question, she is known also to have made use of a leaf nest about 100 yards distant.

From the management standpoint, hollow trees are doubtless desirable even though squirrels can live without them. They protect the animals from hunters, natural enemies such as raccoons* and owls, and severe weather.

LEAF NESTS

There is considerable variation in the leaf nests built by squirrels. They may be located only ten feet from the ground, or in the topmost branches of tall river-bottom timber. They may be placed in the hollow top of a stub, next to the bole of a large tree, in a fork, or among the twigs of a lateral branch or high stem.

* An enemy by analogy only so far as the present work is concerned.

In the upland woods two species of trees, the black oak and white pine, were conspicuously favored for nesting. In proportion to its occurrence the white pine was most often used. During late July and August 1939 a count was made of all nests in the squirrel woods. A total of 69 were recorded, including all sizes, and 18 of these were in white pine. This species formed only 2.6 percent of the trees over 3 inches in diameter. The remaining 51 nests were in black oaks, which composed 24.2 percent of the woods in the size class mentioned. There was none at all in white oaks. In the squirrel woods 40 nests were in trees over 10 inches in diameter, of which 32 were in black oak. Since white oaks in the woods ran considerably smaller than the black, this explains in part the complete failure to use this species. At least two nests in the woods had been in white oaks the year before, and they were often used elsewhere. However, where black oaks were common the squirrels



Fig. 6. An old white oak den tree amid the smaller second growth.

showed a decided preference for them as nesting sites. The black oak drops its leaves in the fall and the white oak often retains them until spring, but whether this has any bearing on the matter is not known.

In 1938 every nesting tree in the woods was climbed, and statistical data taken on the nests. Nineteen of the largest and most usable structures averaged 30.1 feet in height above ground. The average diameter at breast height of the trees in which these were placed was 10.3 inches.

Other species of trees in which nests have been observed are American elm, beech, hard maple, large-tooth aspen, basswood, red oak, sycamore, hemlock, red maple, black willow, and black ash. It is my impression that in the selection of nesting trees, size, location, and probably factors of suitability known only to a squirrel are more important than species.

For nest materials the fox squirrel usually uses twigs, cut green, and leaves. Ordinarily these are the only components. However, I have found nests made in part of pine or hemlock twigs and needles. In the river bottom there were nests constructed almost entirely of shredded grape bark, and several contained a portion of the fibrous inner bark of the large-tooth aspen. A small amount of grass or moss is occasionally included in nests, but material from the ground evidently is not favored. One of the nests examined contained a square foot of old burlap, and another a few corn husks. On January 21, 1939, I found a female squirrel in a nest 29 feet up in a 9-inch black oak. The nest was built of black oak leaves and twigs and lined with pieces of a newspaper dated April 9, 1938. Usually there is no particular lining in a leaf nest. The leaves with which it is built become frayed and form a soft inner layer.

The animals usually get the bulk of the twigs for a nest from the tree in which it is built. Some twigs from neighboring trees can often be found, however, and in one case aspen bark was probably carried more than 100 yards to a nest.

Most nest building activity occurs during the summer. Some nests, however, are built in late winter and spring before the leaves come out. Such structures sometimes have a characteristic appearance distinguishing them from summer-built nests (Figs. 7 and 8). The outermost portion is a criss-crossed framework of bare twigs with dead leaves packed inside to form the nest. Later in the year squirrels clip twigs with the leaves attached, and these give a nest a more bulky appearance than in the former case (Fig. 9). Summer nests are packed with layer upon layer of green leaves that retain their color inside until the following spring. These leaves dry in place and make an excellent shelter. In some winter nests, twigs of white oak with their unshed leaves are used. Although these differences are sometimes usable criteria in judging the age of a particular nest, the types are not well enough defined to make quantitative work on this basis practicable.

It was found that there is a gradual progression of nest sizes, from a mere handful of leaves to a large bulky structure with a cavity. Some of the

abortive starts may represent cutting and piling as a reaction to the nest-building instinct—possibly by young animals. Many of them appear never to be used for anything. In the squirrel woods every stage of decay and construction was found. What to call a nest was difficult to decide. It was this fact that caused me to abandon, at least temporarily, a notion that nest counts might be used as population indices.



Fig. 7. A winter-built nest in a black oak on February 26, 1939. Stubs from which twigs were clipped can be seen.



Fig. 8. A small compact winter-built nest showing entrance hole (March 11, 1939).

Fig. 9. A nest in a black oak on February 26, 1939. This structure was built in late summer (1938) of green twigs with the leaves attached.



In the large nests, suitable for habitation in winter, the cavity is ordinarily 6 to 8 inches in diameter and somewhat flattened vertically. Some have a well-defined opening in the side (Fig. 8) but more often it is partly covered by leaves or is indistinct. The compact portion varies from about 10 to 18 inches in diameter, but often departs from the common globular shape.

Many nests have new twigs and leaves added to them from time to time. Some are completely rebuilt with the old nest as a platform and the new

structure on top. Others are allowed to weather away with only a twig added now and then, apparently by some half-interested animal. Some nests, built in summer, are used continuously through the following spring and have young born in them.

From the ground, most leaf nests look small and flimsy, although a closer examination shows that they are by no means so frail as they appear. On several occasions after a rain I evicted a squirrel and found its nest to be dry and warm. Nests that are not regularly used soon cave in and in wet weather become thoroughly soaked.

Breeding

Published information on the breeding of fox squirrels is relatively incomplete. Although the animals are often kept as pets, I know of no report on their breeding in captivity. Some of the first observations were made by Audubon and Bachman (1849), who stated that copulation occurs in December and January and that the young are brought forth at the beginning of March, or earlier, and on into April. They asserted that nests containing young are invariably in hollow trees and they had reports of two broods per season. Brayton (1882) observed that fox squirrels are usually monogamous and bring forth about three at a birth, with two broods per season. Stoner (1918) found that young may be born in leaf nests and suggested that in some instances there are two litters in a season. About the only specific records cited are those of Stoddard (1920), who climbed trees and examined leaf nests in northwestern Indiana. He gave four brood records for March and April and stated that he had never found a second litter later in the season. The gestation period of the fox squirrel is not definitely known, although Lyon (1936) said that from analogy with the gray squirrel it is probably near 45 days.

SEX RATIO

In the studies at Allegan 728 individual fox squirrels of known sexes were handled between September 1937 and December 1939. In this series 324 were males and 404 were females. Table 3 gives the methods by which these animals were taken and the percentage of the sexes in each group.

In this series of squirrels there is a material preponderance of females. This is due to the fact that many more individual female animals were taken in the box traps. An examination of the total catch record by months (Figs. 10 and 11) indicates that at two seasons, August and January, the sexes were nearly equally represented, and that the difference in the total ratio may be due to the fact that the traps were less attractive to males than to females during most of the year. The percentage of recatches in the two sexes shows that this probably is true. Among the animals taken by box trapping 62 of the 286 males (21.67%) repeated at least once, were taken a total of 178 times, and averaged 2.87 catches per animal. Of the 374 females, 112 (29.9%)

repeated and were taken a total of 344 times, giving an average of 3.07 for each female.

Thus, 8.23 percent more of the females were recaptured than of the males, and this in spite of a much higher trap mortality among the former. A total of 83 squirrels died in the traps, of which 23 were males and 60 were females.* This would disproportionately reduce the females in the population and hence the chances for female repeats. It is probable that the potential number of repeating females is even larger than the 29.9 percent in this series.

The greater tendency of females to repeat, probably, though not necessarily, indicates that proportionately more animals of this sex were captured in the first place. It appears likely that the trap-wariness, lesser activity, or whatever it is among the males, obscures, in this study, the true sex ratio existing in the wild.

As to the fluctuation in the sex ratio among trapped animals (Fig. 11) there appears to be no good explanation at present. It is roughly correlated with the breeding season, and yet there are points of variance that tend to discourage speculation. It is likely that considerably more work will need to be done before we have a completely satisfactory answer to this problem.

Although, from the foregoing, it appears that there is an explanation for the preponderance of females in the catch by trapping, females were also more numerous in the litters of young. There were 23 broods of callow young and embryos from 1938 and 1939 which could be sexed by macroscopic methods. In this series there were 26 males and 34 females. It is unfortunate that these figures are too small to be significant, for they suggest that the high catch of females may not have been all due to trap-reaction.

TABLE 3.—Sex Ratio Among Fox Squirrels Handled 1937-39.

How taken	♂	♀	Total	♂	♀
Shot	11	8	19	57.9	42.1
Highway kills	14	9	23	60.9	39.1
Taken from nest	10	10	20	50	50
Predator kills	1	3	4	25	75
Found dead	2	0	2	100	00
Box traps	286	374	660	43.3	56.7
Total	324	404	728	44.51	55.49

* This mortality was distributed throughout the year, except that it was greatest in late winter among pregnant and lactating females. Most of the trap losses among squirrels occurred in the rabbit and raccoon traplines which, due to their extent, could be operated only once daily. Losses were practically eliminated in the squirrel woods by running traps in late morning and just before sundown. Good use was made of the dead squirrels, which would have been collected for autopsies had they not been available as trap losses. Figures from the other traplines are, of course, unreliable for population estimates.

TABLE 4.—Frequency Distribution of Recatches by Box Trapping.

Times taken	1	2	3	4	5	6	7	8	9	18	22	Total Individuals
Males	224	38	14	6	2	0	0	1	0	1	0	286
Females	262	66	21	11	6	0	3	3	1	0	1	374
Totals	486	104	35	17	8	0	3	4	1	1	1	660

Total times squirrels were handled in box traps—1,101.

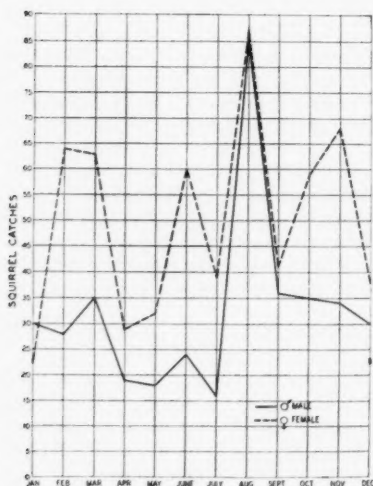


Fig. 10. Total squirrel catches for the two years 1938 and 1939. From these data it appears that there were four rather definite seasonal fluctuations in the effectiveness of box traps baited with ear corn. These periods were more marked in the male. The most noticeable season during which it was difficult to take the animals came in April and May.

PHYSICAL CHARACTERS

The information on sexual condition with reference to breeding and age is by no means complete, and some of the characters indicated here must be tested further to determine to what extent they may be fallible.

This work has definitely established that Michigan fox squirrels have two main breeding periods—one in January and February, and the other in June and July. By winter, then, the population is composed of old males and females, and young of the year from each of these two breeding periods. In December an old squirrel in good condition often weighs from 1 pound 10 ounces to 2 pounds. A spring juvenile can be expected to weigh from 1 pound 6 ounces to 1 pound 10 or 11. A summer juvenile may weigh from 1 pound to 1-6. These generalizations by no means hold good in every case. Weight varies materially with the condition of the animal, which depends in part upon the habitat and, in all probability, the particular season. Weight is merely one of the characters useful in deciding to what age group a squirrel belongs.

When a young squirrel leaves the nest the soles of its hind feet are heavily furred. This wears off after the animal has traveled about for a while. For a time I thought that the amount of hair on the feet in the fall would serve in helping to distinguish the summer juveniles, from the first litter, and from the old animals. However, it was found that some old squirrels get a new growth of fur on the feet that is very heavy by mid-December, and by late winter there is such a variation in conditions that the character is of little value in determining age.

The sexual cycle and breeding of males: Among winter fox squirrels a considerable variation is found in the extent of the furred area on the scrotum. From the appearance of several animals of known age I suspected that this was a cumulative condition, and that as squirrels grew older they progressively shed the scrotal fur. There is a graded series of conditions from that shown in Fig. 12 through that shown in Fig. 14. That the extent of the bare area on the scrotum could be used as an age character was considered logical, especially in the light of a report by Johnson, Foster, and Coco (1933) that such a condition existed in the spermophile. Among fox squirrels it seems to hold fairly well that young animals average more hair on the scrotum than old ones. There are known cases, however, of yearling squirrels that closely approximated the condition of the animal shown in Fig. 14.

An entirely new light was thrown on this matter by several squirrels handled during 1940 at the Rose Lake Wildlife Experiment Station in conjunction with D. F. Switzenberg. These specimens were sloughing the black wrinkled skin of the scrotum in August, and a new growth of hair could be seen coming in. The new skin of the sac showed only a light pigmentation, and in late summer such an animal might, as far as these characters are concerned, be mistaken for a spring juvenile. But even though the testes were

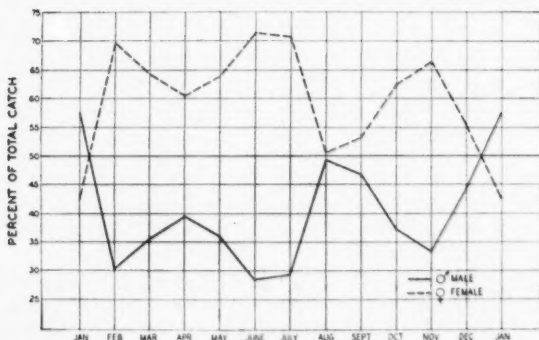


Fig. 11. Percentage of male and female fox squirrels handled in the total catch for 1938 and 1939. The sexes were most nearly equal in August, and in January males exceeded females. The latter represents a reversal of the trend during the remainder of the year. A good explanation of this difference in activity and/or trap-wariness is not apparent, although there is a rough correlation with the breeding seasons.

reduced in size, the loose sac-like condition of the scrotum in old squirrels was apparent when it was compared with that of developing young of the year.

Although the scrotal character is not trenchant, and some individuals are definitely "in between," during the winter it has value in aging squirrels, especially to an experienced worker.

In most summer juveniles the testes are abdominal during the winter months. As a result the scrotum will not have assumed the semi-pendent condition and will appear as in Fig. 12. The beginnings of the black area can be seen only when the fur is parted.

Male fox squirrels may undergo testicular enlargement as early as September and October, although the condition becomes more marked in November. During the fall the scrotum usually measures 1 inch to $1\frac{1}{2}$ inches in length. This is a rough measurement easily recorded in the field. After enlargement begins the testis is turgid and in old males at this season measures 20 to 25 mm. exclusive of the epididymus. But as late as October some animals have the testes reduced, proportionately long, and considerably more flaccid than after they begin to enlarge. For example, on September 19, 1937, a squirrel was taken in which the testes averaged 22.7 mm. in length and weighed 1.65 grams. This animal was already approaching breeding condition. On October 5 another individual was autopsied in which the testes averaged 20.4 mm. in length, were flaccid, and weighed only .76 grams. The latter specimen was apparently still sexually dormant. Both appeared to be old animals.

By mid-December, and possibly earlier, some animals are in full breeding condition.* Externally the scrotum is a full inch and three-quarters in length (45 mm.) and the testes measure 28 to 30 mm. A fully developed testis weighs between 3 and 4 grams with the epididymus removed. When the animal is ready to breed, the latter is much enlarged and gorged with sperm (C, Fig. 15). The epididymus, and in particular the tail and the mid-portion, is considerably smaller in animals that have not reached the height of the sexual cycle (B, Fig. 15). Some old animals are ready to breed in early December, at least two weeks before the earliest oestrus in females. Many individuals are later, however, and it is likely that some are not yet ready for copulation in the middle of January. A good example of the development of an old male is that of number 44423 taken first in the squirrel woods in October 1937. This animal was at the full sexual development when caught on December 21, 1938. It was autopsied on January 16, 1939. On this date its testes measured (L) 29×15.6 and (R) 28.9×15.7 . One of them weighed 4 grams and was one of the largest testes recorded.

Among spring juveniles of the year the testis is usually from 15 to 19 mm. in length during October and November and proportionately larger in December. Some of these animals will be found still short of maximum development in February and March, although I believe that most of them breed at this season. Due to the small number of repeat records on marked animals these

* A few squirrels have fully enlarged testes in October, but whether they are capable of breeding so early in the season is not known.

deductions are based to a great extent upon the examination of individuals of which the age was not known for certain. At maximum development the testes of year-old squirrels probably average several millimeters smaller than they would be a year later when the same individual might be classed as an "old" animal. The testes of what appeared to be twelve adults taken from December to February averaged 28.22 mm. in length. The testes of seven yearlings taken in February and March averaged 26.09 mm. All were evidently in full breeding condition.

Some squirrels are ready to breed during April and May. For example, squirrel 310♂ was taken as a juvenile on August 14, 1938, when it weighed 1-8. On the following April 4, the animal was in full breeding condition (weight 1-12). I do not know whether these are late-breeding spring juveniles of the year before, early-breeding summer juveniles, or animals born between times.

During the winter breeding season a group of young squirrels will be found with testes in the coelum and usually measuring from 10 to 16 mm. in length. These are summer juveniles. One example of a clear-cut case is that of squirrel 44416, a summer juvenile, taken in the squirrel woods in October, 1937, when it weighed 1 pound, 2 ounces. This animal was taken seven more times until January 25, 1938, when it died and was autopsied. The testes measured 16 and 16.5 mm. in length. This was probably a young animal from an early summer litter.

I have no indication of any of the summer generation coming into breeding condition in the winter period. There is little doubt that they breed for the first time in the June and July season, or possibly in some cases during May. One squirrel that was almost certainly a summer juvenile of the year before was found in full breeding condition on May 3, 1938. Figure 15 shows three pairs of testes from specimens taken in early February (1939) which illustrate the relative size of a summer juvenile compared with a spring juvenile and an old animal. The age of these squirrels was judged by their condition.

As before indicated, there is a considerable diminution in the size of the testis after the breeding period. The epididymus shrinks, the gland declines in girth and length, and becomes flaccid. Not a large number of male animals were autopsied in late spring and summer, and hence my data for this period are few. What apparently was a squirrel at the "low" of the sexual cycle was a specimen taken July 13, 1939. Measurements of the fresh organs were (L) 19.3 x 7.1 and (R) 20.5 x 6.6. One of these glands weighed .49 grams. In another animal in the same condition on September 5, 1939, the testes measured (L) 19.6 x 7.8 and (R) 20.7 x 7.5. One testis weighed .66 grams (weights after preservation). In what appears to be the dormant condition the gonads are longer in proportion to width than when developed and are flaccid as compared to the turgidity of the fully enlarged organ. I have examined some males between breeding seasons in which the testes were nearly as large as in winter. On this point Mossman, Lawlah, and Bradley (1932) record that they took both gray and fox squirrels with large testes at nearly

all seasons of the year. From this they deduce that the cyclic atrophy and hypertrophy of the organs is not marked. I cannot entirely agree with this, for as previously pointed out, in some squirrels the testes are reduced to one-sixth or less of their breeding weight.

Among the specimens examined none is known definitely to have had fully enlarged testicles twice in the same year. Several adult males were found with the gonads in a reduced or declining condition from May to July. It is probable that these individuals had bred early in the year but not in the second period. On the other hand, since some females breed twice, it might be expected that at least some of the males would do so also. Possibly it is the young males that breed only once in their first year.

Due to the nature of the data, complete conclusions on the breeding cycle of male fox squirrels cannot be drawn. The investigation has, however, as should all such studies, opened up numerous problems that can be attacked with a more concrete objective than would have been possible before. It will be profitable to consider what sort of behavior pattern these observations fit and in what direction future work would best be aimed.

A certain group of old squirrels come into condition in December, and most of them apparently breed in January. They may or may not breed a second time. Other males, principally yearlings and some old animals, come into condition during January and February or possibly later. Some will be at sexual "high" during March or April. These may be the sexually dormant animals found in June and July. Possibly the old males and this group breed early the following winter. Juveniles born in the summer do not breed in the following winter season and will be found developing during the late winter and spring months. They breed in the summer, or possibly late spring, for the first time. It may be that these squirrels, which are now adult, go into a period of inactivity and do not develop early in the fall. They may be the adult animals that are found sexually quiescent in September, October, and November, and the individuals that breed late in the winter season.

Although some of the above is unsupported by precise records, it gives us a fair idea of what conditions may exist and what to look for in the future.

The sexual cycle and breeding of females: Among fox squirrels, sexually inactive females have the vaginal orifice closed dorsally by the adherence of the lips of the vulva.* The uterus is thin-walled, relaxed, flattened, one to two millimeters wide, and crumpled in the pelvic cavity. At the time of oestrus the vulva is swollen, its walls are parted, slightly protuberant, and reddish in hue. The uterus at this stage is round in cross section, about three millimeters in diameter, and much congested. Follicles are apparent on the ovaries.

Young female squirrels that have never borne a litter of young have the nipples small, flat, and without pigment. In a female that has suckled young the teats are larger and have black pigment at the tip. In summer the hair

* Stockard (1934) reported a similar condition in the prairie dog, *Cynomys leucurus*.

around the nipples become worn and matted. Thus a juvenile female, which has never bred, can be distinguished from an old animal by the mammae. In fall and winter old females that bred in spring but not summer have the teats greatly reduced, but even in these animals a trace of pigment usually is discernible at the tip of the flattened nipple.

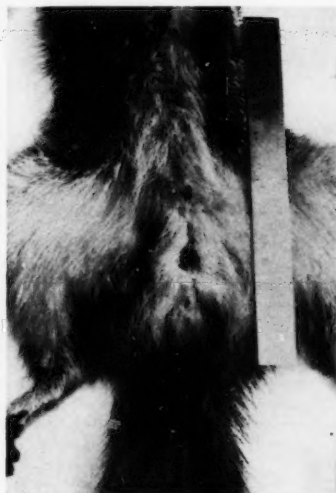


Fig. 12. Scrotal area of a summer juvenile in February. The hair has been parted to show the beginning of the dark pigmented tip of the scrotum.



Fig. 13. Scrotum of a yearling in February. In this specimen the sac is still heavily furred. Although some yearling squirrels will, by late winter, approach the condition shown in fig. 14, the character has been found sufficiently constant to be useful.

The teats of a female squirrel develop rapidly after insemination. They swell and the tips become black-pigmented. The glandular tissue spreads out under the skin and becomes a continuous layer over the ventral surface of the body. The mammae are eight in number (one specimen was found with nine), and the four pairs, from their position, may be designated as: pectoral 1, pectoral 2, abdominal, and inguinal (Fig. 16). The abdominal pair is first to develop and the pectoral 1 last. The order is usually abdominal, inguinal, pectoral 2, and pectoral 1; however, the pectoral 2 and abdominal pairs may be equal, and in some cases the former precedes the latter in development. Sometimes the anterior pair does not appear to be functional. Milk can be squeezed from the nipples just before the birth of the young and for some

time after they are weaned.* Just how long it takes the average squirrel to "dry up" I do not know; but milk can be found, in some cases, more than three months after parturition.

Pregnancy can be detected easily by palpation (see Haugen on rabbits, 1940). In some specimens it is possible to count the embryos, although this type of data has not been used in computing the number of young. In late winter and spring the condition of the mammae is at first sight an indication of whether the animal is carrying or has borne young. In non-breeders the teats are inconspicuous.



Fig. 14. Scrotum of an old squirrel in February. Much of the hair has been shed and the scrotal sac is dark and wrinkled. This black skin will be sloughed in summer when a new growth of hair comes in. (Left.)

Fig. 15. Testes of summer juvenile (A), yearling (B), and an old animal in February. In each pair one testis has the epididymus removed. In (C) the latter organ is swollen with sperm. (B) does not appear to be in full breeding condition. (Right.)

BREEDING SEASON

The earliest indication of sexual activity among females is a record of December 24, 1938. An animal was taken on that date showing a condition approaching oestrus. The earliest actual breeding record comes from a litter of young found in the nest on February 19, 1939. One of these weighed 28.89 grams and was probably about 7 days old. If Lyon's (1936) estimate of a 45-day gestation period is correct, copulation took place in the last week of December. Another juvenile was found in a nest on February 28. This animal weighed 36 grams and was probably near 11 days old, indicating breeding about January 3.

The main breeding period early in the year lasts from the first days in

* Probably at ten to twelve weeks of age.

January to the first week in March,* with sexual activity greatest in late January. Tables 5, 6, 7, 8, and 9 summarize records obtained from the examination of females during 1937, 1938, and 1939. Of 13 April females autopsied but not recorded in the tables, 10 were lactating, 2 were sexually dormant summer juveniles, and another animal had not bred, possibly due to a bad case of mange.

Between January and June a total of 21 females were handled which apparently had not bred. Most of these were summer juveniles of the year before (examples: S. C. 307, 308, 309, 321, 332, 362, 383);** but the age of several was uncertain, and two might well have been old animals. It is also possible that of the eight sexually inactive animals examined in February some might have bred in March or later, as they were not retaken for further observations. Although one old animal (previously tagged) is known to have been still sexually dormant on February 13, it is fairly certain that most of the late breeders were yearling animals which had not previously borne young. That some of these yearlings breed early, however, is shown by the records of four known to have been pregnant by February 15.

There are fewer records on the second breeding period, and nearly all of these are from 1939. Apparently the height of the sexual activity is in late June and early July, although some breeding occurs earlier than this and some later. One advanced pregnancy on June 25 indicated breeding about mid-May. Three animals are known to have bred about mid-July and one was found in an early pregnancy on July 27. Most of these latter would have borne in late August. It is not improbable that some young squirrels are brought forth in early September.

One female which was, from appearance, a summer juvenile of the year before was found in or near the oestral condition on June 24. Another young animal was pregnant on June 28. Squirrel 44415, which was known to be an old animal, bore one litter soon after March 1 and was lactating again on August 6. On October 2 she was still lactating and was drying up when handled on October 13. This squirrel was entirely dry when taken on November 6. One old female that was lactating on September 1, 1938, was pregnant again on March 5, 1939.

A total of 15 squirrels are known to have borne two litters of young in the same year. These animals were either taken during both breeding periods or were found pregnant in the summer with the nipples showing that one litter had already been suckled. Fourteen squirrels are known to have had a summer litter but were not taken in the spring. Twenty-one females were handled at such times that they are known to have had a spring, but not a summer, litter.

* In 1939 two females in very early pregnancy were handled on March 5 and March 15 respectively. Chronologically this agrees with several records of males in full breeding condition at this time.

** Numbers in the autopsy catalog of the Swan Creek Wildlife Experiment Station.

Due to the small number of repeats among marked squirrels, not enough data are available to prove or disprove these points; but the indications are that old healthy squirrels usually have two litters of young and that most of the young animals breed only once their first year. The latter probably breed when about 11 months old. Spring juveniles are known to have bred in the late winter period and all that were definitely established as summer juveniles are known to have skipped this period. As some squirrels breed for the first time in summer it is logical that these are the summer juveniles. Just one

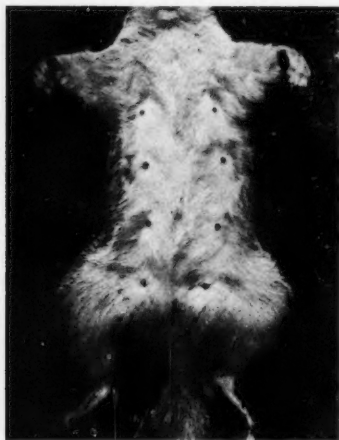


Fig. 16. Mastology of a fox squirrel. This specimen was a lactating female in April.

TABLE 5.—Summary of Breeding Data from Females Autopsied in January.

Date	Autopsy*	Age		Embryos		Length	Weight	Remarks
		Female		Left	Right			
1-12-38	97	?		0	0			Sexually dormant.
1-13-39	239	Ad.		0	0			Uterus enlarged.
1-15-39	242	Ad.		0	0			Uterus enlarged, vulva swollen.
1-15-39	243	Ju.		0	0			Sexually dormant, vagina closed.
1-17-37**	?		0	0			
1-20-39	247	Ju.		0	0			Uterus slightly turgid, vagina closed.
1-21-37	?		0	0			
1-21-39	246	Ad.		0	0			In breeding condition.
1-22-39	250	Ad.		0	0			Uterus swollen.
1-24-38	101	Ad.		1	3			Embryos minute.
1-30-39	267	?		0	0			Sexually dormant.
1-31-39	271	Ad.		0	4			Embryos minute.

* Autopsy numbers are from the Swan Creek series.

** All 1937 autopsies are from the Kellogg Farm (Allen 1938).

animal was followed for a sufficiently long period to verify the evidence as to the litters per year as correlated with age. Squirrel 44415 was a spring juvenile in 1937. It bred in the late winter of 1938 but not a second time in the summer. In 1939 it bred both in late winter and in early summer.

There is evidence that poor health may impede the breeding of a squirrel. Two animals appearing to be adults had extensive mange (or what appeared to be mange) over the body and failed to breed. Another extremely emaciated animal which was handled had not bred.

TABLE 6.—Summary of Breeding Data from Females Autopsied in February.

Date	Autopsy* Female	Age		Embryos			Weight	Remarks
		Left	Right	Length	Weight			
2-1-37	?	2	1	3.5			
2-1-39	268	Ju.	0	0				Sexually dormant.
2-3-39	277	?	0	0				Uterus enlarged.
2-5-38	94	Ad.	0	0				Uterus slightly enlarged.
2-5-39	279	Ad.	2	1				Embryos minute, uterine enlargements 6 mm.
2-5-39	280	Ad.	1	2				Embryos 23 somites.
2-6-39	282	Ad.	1	3				Enlargements 18 mm.
2-6-39	283	Ju.	1	1				Enlargements 4 mm.
2-6-39	291	Ju.	1	2				Enlargements 12 mm.
2-6-39	292	?	4	1				Enlargements 12 mm.
2-6-39	293	Ju.	2	1				Enlargements 10 mm.
2-6-39	295	Ju.	1	2				Enlargements 14 mm.
2-7-39	296	Ju.	2	1				Enlargements 14 mm.
2-7-39	302	Ad.	3	0	32.4	3.8		
2-8-39	301	?	1	2				Enlargements 17 mm.
2-8-39	303	?	0	3	33.4	3.5		
2-9-38	107	Ad.	0	0				In oestrus.
2-10-37	1	2				Embryos minute.
2-10-38	108	Ju.	0	0				Approaching oestrus.
2-11-39	307	Ju.	0	0				Sexually dormant, summer juvenile.
2-11-39	308	Ju.	0	0				Sexually dormant, summer juvenile.
2-11-39	309	Ju.	0	0				Sexually dormant, summer juvenile.
2-13-38	109	Ad.	0	0				Sexually dormant.
2-14-39	320	Ad.	2	1	25			
2-14-39	321	Ju.	0	0				Sexually dormant, summer juvenile.
2-17-39	325	Ad.	1	2	44	6.81		
2-20-37	2	1	22			
2-20-38	0	2	29.4	1.72		
2-22-37	1	2	38			
2-22-39	327	Ad.	1	1	41.5	6.23		
2-23-39	332	Ju.	0	0				Sexually dormant, summer juvenile.
2-24-39	329	Ad.	2	1	57	16.38		At full term.
2-24-39	330	?	0	3	29.2	2.33		
2-26-38	0	2	24	1.45		

TABLE 7.—Summary of Breeding Data from Females Autopsied in March.

Date	Autopsy	Age		Embryos			Remarks
		Female	Left	Right	Length	Weight	
3-2-37	0	3	Embryos minute, enlargements 11 mm.
3-5-39	344	?	2	2	47.5	10.76	Lactating.
3-6-37	?	Lactating.
3-6-37	?	Lactating.
3-6-38	114	?	0	0	Bad case of mange (?).
3-6-38	123	?	0	0	In oestrus.
3-7-37	?	Lactating.
3-7-39	352	Ad.	2	1	51.8	9.25	Lactating.
3-11-39	348	Ad.	(2)	(1)*	Lactating.
3-12-37	?	Lactating.
3-12-39	349	?	0	0	Lactating.
3-12-39	350	?	(2)	(1)	Lactating.
3-14-37	?	Lactating.
3-14-39	351	Ad.	Lactating.
3-16-39	353	Ad.	Lactating.
3-16-39	354	Ad.	(2)	(1)	Lactating.
3-17-39	355	Ad.	Lactating.
3-21-37	Ju.	0	0	Sexually dormant.
3-22-37	Ju.	0	0	Sexually dormant.
3-22-39	362	Ju.	0	0	Sexually dormant, summer juvenile.
3-22-39	372	?	Lactating.
3-25-39	361	?	Lactating.
3-29-37	Ju.	0	0	Sexually dormant.

* Parentheses indicate uterine swellings after birth of young. Parturition had probably occurred in these cases within two days.

TABLE 8.—Summary of Breeding Data from Females Autopsied in July.

Date	Autopsy	Age		Embryos			Remarks
		Female	Left	Right	Length	Weight	
7-11-39	424	Ad.	0	0	Had a spring litter.
7-19-38	158	Ju.	2	1	Embryos minute, first litter.
7-22-39	444	Ad.	1	1	31.4	2.58	Second litter.
7-22-39	460	Ad.	0	0	Had spring litter.
7-27-39	453	Ad.	1	2	39.8	8.45	Second litter.
7-30-39	456	Ad.	3	0	15.6	..	Second litter.
7-30-39	457	Ad.	1	2	48.6	13.45	Second litter.
7-30-39	459	Ad.	(1)	(1)	Second litter.

TABLE 9.—Breeding Records Obtained by Autopsies and Field Examinations of Female Fox Squirrels.

	Females					
	Calculated Copulation Records	in or Approach- ing Oestrus	Records of Pregnancy	Records of Birth	Females Lactating	Females "Drying up"
Dec. 22-Dec. 31	1
Jan. 1-Jan. 10	5
Jan. 11-Jan. 20	6	9
Jan. 21-Jan. 30	10	1	1
Jan. 31-Feb. 9	9	3	9
Feb. 10-Feb. 19	1	1	27	..	2	..
Feb. 20-Feb. 29	3	1	5	1	1	..
Mar. 1-Mar. 10	..	3	12	4	8	..
Mar. 11-Mar. 20	1	5	8	..
Mar. 21-Mar. 30	1	9	..
Mar. 31-Apr. 9	9	..
Apr. 10-Apr. 19	1	9	..
Apr. 20-Apr. 29	2	..
Apr. 30-May 9	1
May 10-May 19	1	1	1
May 20-May 29
May 30-June 8	2
June 9-June 18	1	1	3
June 19-June 28	3	1	3	..	1	..
June 29-July 8	2
July 9-July 18	3	..	2
July 19-July 28	1	..	5	2
July 29-Aug. 7	4	..	1	..
Aug. 8-Aug. 17	3	..	1	..
Aug. 18-Aug. 27	1	..
Aug. 28-Sept. 6	1	..	3	..
Sept. 7-Sept. 16	3	..
Sept. 17-Sept. 26	2	1
Sept. 27-Oct. 6	2	2
Oct. 7-Oct. 16	1	1
Oct. 17-Oct. 26	1	..

FECUNDITY

From 1937 through 1939 I obtained a total of 51 brood records on the fox squirrel. Of these, 38 were sets of embryos and 13 were litters of young found in the nest. Table 12 gives the distribution of records over the three years. Only in 1939 were enough data secured to give a significant figure on average number of young for a single year.

TABLE 10.—Number of Young per Litter.

	Embryos		Nest Records		Total litters	Total young	Mean
	Litters	Young	Litters	Young			
1937	6	17	3	9	9	26	2.89 ± .20*
1938	4	11	0	0	4	11	2.75 ± .48
1939	28	85	10	27	38	112	2.95 ± .12
Totals	38	113	13	36	51	149	2.92 ± .10

* In all calculations standard errors are used.

Although the number of young per birth is known to fluctuate from year to year in some animals (see Alcorn 1940, on the Piute ground squirrel), as far as these records go it is apparent that the fox squirrel in Michigan averages about three young per litter. The productivity of a breeding stock probably will depend upon the number of old females in the population; for these studies indicate that most old animals average nearly six young per year, and yearlings produce about three. Some spring yearlings may, possibly, breed twice their first year, although none did so among the animals adequately recorded in this work. Since I have no quantitative measurement of the age ratios existing in the population, it is not possible to say just what increase could be expected from a breeding stock of a given size.

DEVELOPMENT OF THE YOUNG

As has already been noted, a female fox squirrel may bear her young in either a hollow or a leaf nest. Hollows appear to be preferred where they are present. At Allegan broods were found in leaf nests dating, at least in part, from the previous year. Evidence is good that one squirrel bore both of her broods in the same hollow in 1939.

As judged by the few records at hand, young fox squirrels at birth weigh 14 to 17 grams. The heaviest embryos examined weighed 16.38 grams. On April 9, 1939, a captive female bore a litter in a nesting log in one of our pens. One young had been born when the female was examined at 10 a. m. and the other was present at 10:30. Eight hours later they weighed 14.66 and 14.71 grams, respectively. Both were females. These young apparently were not cared for by the mother and were dead two days later.

Another captive female bore a litter sometime between February 28 and March 8. One of the young weighed 23.6 grams when the litter of three was discovered. These juveniles were reared in captivity until they died, apparently of scabies, on April 28. Their eyes were first open on April 7, when they were near 5 weeks of age. At the time of their death these young could climb about a little, but I do not believe that any of them had been out of the nest by its own efforts. Seton (1929) and Lyon (1936) stated that young fox squirrels begin to come out of the nest at 10 or 12 weeks of age. My information tends to agree with this.

A female squirrel was killed by a car in Allegan in April 1938, and her two young worked their way out of the knot-hole nest in a sycamore and were found on the ground. They were out of the nest and unfed at least a day when I got them on April 16. They were both males and weighed 135 and 149 grams, respectively. The smaller died, but the other was kept until it escaped in mid-June.

This young squirrel was not yet weaned and was fed undiluted evaporated milk until the middle of May. At this time it could eat cereal, nut meats, fruit, etc. By June 7 it could open walnuts. This animal could hardly have been over 8 weeks old when received, and probably was not less than six. Judging from the development of this specimen, weaning must occur, or at

least start, at about 10 weeks of age. Whether a mother fox squirrel brings any food to her nest of young I do not know, but Seton (1929) says they have not been known to do so. That the female moves them readily is indicated by the fact that we have never been to able to check the same litter twice. They have been shifted elsewhere each time they were disturbed. Gaige (1922) witnessed a female moving her naked brood of two from a house that was being dismantled in Ann Arbor on September 13, 1922. Lang (1925) described a method by which they are transported. On one occasion a female came in response to the squeals of a still-blind juvenile that Stuewer had just removed from a hollow in the riverbottom.

The earliest we have taken a juvenile of the year in a trap was on May 21, 1939. This animal was probably between 12 and 14 weeks old. Few juveniles appeared in the traps before the middle of June and they were not common until July. In the fall the earliest juvenile of the summer litter was taken on October 17, 1939. They are much more common in November and December.

From these rather sketchy indications it appears that young squirrels are not self-sustaining until they are between three and four months of age. This is a point of importance, considering that there are late summer litters and that the Michigan hunting season opens on October 15. Work is now being done to determine how much fall mortality there may be among squirrel broods orphaned in the shooting season.

Disease and Parasites

Early in the spring of 1936 at the Kellogg Farm (Allen 1938) a number of squirrels were seen which had an appearance of mange, having lost a part or nearly all of their hair. This condition among squirrels became conspicuous and had every appearance of an epidemic. In the following winter populations were found to have dropped off somewhere between 30 and 50 percent.

Since that time, in conversations with residents of various counties, I have had "naked" squirrels reported from nearly every portion of the southern part of the state. In the Allegan studies an effort was made to get more information on this disease.

The hairless condition is, at least in some cases, associated with an infestation of the scabies mite, *Sarcoptes scabiei* subsp. This is the identification given it by S. C. Whitlock and W. C. Gower from specimens examined in the department pathology laboratory. In some cases mites could not be found, and even when they were present in large numbers it is not certain whether they were a primary or secondary factor. For convenience I have referred to this disease as scabies, with the understanding that its exact nature is yet to be determined.

In many animals the scabby condition appears first on the ears. The tip and rim of the ear become bare and dark. This is followed by swelling and the appearance of scabs and sometimes pus. At times the crease between the ear and head becomes an open sore. This may involve the entire ear, which



Fig. 17. Head of a scabby squirrel. The ears are turned back, with open lesions between the head and ear.



Fig. 18. An extensive case of apparent sarcoptic mange. Mites could not be detected in every case.

is drawn down and stuck fast to the head (Fig. 17). In other cases a spotty hairlessness occurs on the head or elsewhere on the body. Considerable itching is manifest and the animals scratch themselves with vigor. In well-developed cases scabs form over the body, and after a time the skin becomes pigmented. Sometimes the pigmentation is followed by a growth of new hair and complete recovery. There are known examples where animals with the shoulders bare as in Fig. 18, or with even a more extensive hairlessness, have recovered and become apparently healthy again. A female in her nest with young in March 1939 had ears in the condition shown in Fig. 17. In the following November she had recovered and her ears were nearly normal.

Scabies as a mortality factor appears to be most important in the winter, although in a record for April or May, Errington (1933) reports finding a nearly hairless fox squirrel dead in the woods with no marks of violence. In the winter of 1935-36 a report came to me of a mangy squirrel that had died in a nest box beside a cottage in Midland Park on Gull Lake. In January 1936, at the Kellogg Farm, I found a squirrel minus much of its fur, dead in the woods. A dog had also found it and chewed off three of its legs. Eugene S. McCartney of Ann Arbor told me of two cases of mortality among very scabby squirrels during an exceptionally cold period in January or February 1936. These animals had been coming to a window of one of the university buildings for food. In December 1938 a squirrel described as "nearly bare" was found dead in the woods by some boys near Crooked Lake

in Allegan County. In the winter of 1937-38 a mangy squirrel was often seen and fed at the state game farm at Mason. Later, Roy M. Hunt found it dead in a woodshed. On January 20, 1939, the members of a W. P. A. crew found a fox squirrel with scabies dead in Section 35, Clyde Township, Allegan County. On March 13, 1939, F. W. Stuewer found a dead squirrel with scabby head and shoulders in Section 32, Heath Township, Allegan County.

As fox squirrels do not store their food in large caches, they must get out periodically during the winter to feed. Any prolonged cold spell will undoubtedly cause an individual with some of its fur gone to suffer. Anyone who has observed wild animals knows that nearly all species are markedly susceptible to exposure, and that a severe wetting or subjection to extremes of temperature for even a short period often proves fatal. This accounts for the high mortality in our box traps. As will be pointed out elsewhere, fox squirrels often remain in their nests for several days during the winter—possibly a fat individual will ride out a week or more of bad weather in this way—but animals with scabies are usually thin. They doubtless need food in order to maintain their resistance to cold, and it is to be expected that they should sometimes succumb.

To determine the degree of emaciation that usually accompanies this hairless condition, the weights of all adult animals showing extensive cases have been selected out and averaged. Table 11 gives the result.

TABLE 11.—Seasonal Weights of Squirrels with Apparent Sarcopic Mange.

	Males		Females	
	No.	Weight	No.	Weight
Dec. - Feb.	6	738.2 \pm 15.92	11	769.6 \pm 16.39
Mar. - May	20	728.7 \pm 15.97	11	720.6 \pm 29.08
Jun. - Aug.	6	751.3 \pm 38.38	13	715.9 \pm 20.75
Sept. - Nov.	3	697.7 \pm 39.34	3	609.0 \pm 13.43
Totals	35	731.5 \pm 11.76	38	724.0 \pm 14.23

Mean weight of 71 animals 727.70 \pm 13.42. (1 lb. 9.6 oz.)

The mean weight of the 71 squirrels of both sexes can be compared with the mean for healthy adults. The latter was 766.0 \pm 4.33 (1 lb. 11 oz.) for a series of 409 weights. The scabby squirrels averaged 38.8 grams, or 1.35 ounces, less than healthy animals.

That this hairless condition may render a squirrel more susceptible to predation is suggested by Errington (1933): "A widely selective preying upon subnormal wild life is hinted at by the visible condition of some *Sciuridae* taken in April and May 1930 from red-tail nests. Three out of five arboreal squirrels, two out of two Franklin ground squirrels, and perhaps one-third of 42 striped ground squirrels were conspicuously afflicted with a mange-like skin disease which may have caused them to relax vigilance or may have lowered distinctly their vitality."

It is also suggestive that in the present study two of three squirrels captured

by dogs were in this condition. It is probably significant that the author above cited says "visible condition." Doubtless most afflictions go unnoticed, lacking any such striking manifestation as scabies. Dead animals found in the woods are seldom subjected to close scrutiny by a pathologist. On December 12, 1938, I observed a male, number 390, on the ground in the squirrel woods. This animal ran with difficulty and was too weak to climb. I caught it by hand. It died that afternoon in a cage in the laboratory. The ears were swollen and red and there were scabs on the shoulders and in the axilla of the forelegs. This case was not conspicuous, and some other factor than scabies might have caused the animal's weakness.*

In the fall and winter of 1937-38 collections of ectoparasites were made from sixteen fox squirrels. These specimens have been identified by specialists in the various groups. In this series 12 squirrels were found to be host to the louse *Neohaematopinus s. sciurinus* (Mjöberg), and three to a less common species *Hoplopleura sciuricola* Ferris. I am indebted to F. H. Wilson of Tulane University for these identifications. On ten of the sixteen fox squirrels were found mites of the species *Euhaemogamasus oregonensis* (Ewing). These mites occur externally and are not to be confused with the scabies mite (*Sarcoptes*). H. E. Ewing of the Bureau of Entomology and Plant Quarantine identified the mites. Dr. Ewing also named nymphs of ticks taken from two specimens of red squirrels as *Ixodes* sp. Ticks have been found occasionally on fox squirrels, but none has been identified. In the series of fox squirrels ten specimens had fleas of the species *Orchopeas wickhami* (Baker), and two were host to *Conorhinopsylla stanfordi* Stewart. For these identifications I am indebted to Newell E. Good and Frank M. Prince of the U. S. Public Health Service.

The most conspicuous ectoparasites of fox squirrels are fleas, and a few individuals were found with evidence of flea bites on the venter. These insects are also found around the entrance holes of dens frequented by squirrels. Fleas were particularly troublesome to captive animals until I removed the sawdust from their nest boxes. This, and the application of a flea powder containing rotenone, considerably improved conditions. I have had no indication that ectoparasites are a cause of mortality among Michigan fox squirrels.

Predation

On two occasions I have seen a healthy fox squirrel in an open field near a woods, got between the animal and the trees, run it down, and caught it. This, I think, gives a clue to the vulnerability of this species to its natural enemies. I have one record from the Kellogg Farm, and one from Swan Creek, of a redbait hawk rising from the ground near a woods with a fox squirrel in its talons. In the spring of 1938 I took a fresh fox squirrel skull from the nest of a redbait in the Allegan area. In Augusta, Michigan, a trapper

* Squirrels are very susceptible to shock, and sometimes die for no apparent reason while being handled. Possibly they are similarly affected by other causes under natural conditions.

told me of taking what he described as nearly an entire fox squirrel from the stomach of a large hawk. There are also reports in the literature which indicate that the fox squirrel occasionally falls prey to the larger hawks, particularly the buteos (Errington 1933, English 1934).

On May 5, 1939, a young fox squirrel with its eyes not yet open and weighing 60 grams was collected from among the food items brought by the parents to a nest of tethered barred owls. The young squirrel had been grasped by the back and killed by a blow of the closed bill, caving in the rear of the fragile skull. It is interesting to note that Errington (1932) records a juvenile fox squirrel, and two juvenile squirrels (one "suckling") provisionally identified as grays, from the pellet remains at a barred owl nest. It appears not unlikely that these young squirrels were taken from nesting hollows with openings sufficiently large to admit the owl.

Stray dogs have accounted for my only other records of fox squirrel predation. One animal with scabies was killed by a dog at the Kellogg Farm in 1936. Another, also with extensive mange, was taken, while still warm, from a dog near the Swan Creek farm (March 6, 1938). A third record of dog predation was obtained on March 20, 1939, when a lactating female, apparently in good condition, was killed in one of the rabbit quadrats. Tracks in the sand told the story.

Highway Mortality

As any Michigan motorist will attest, fox squirrels frequently meet their end on the roads. In the two years of this work, 23 specimens were picked up by the experiment station staff and a few interested people in Allegan. I believe that the greatest traffic losses occur in cities where the animals live in shade trees along the streets. It is very common to see dead fox squirrels along roads in the country, however, and the total mortality over the state is probably considerable. There evidently is nothing that can be done about it.

Weight and Condition

In calculating the weight of the average fox squirrel, I separated males and females and eliminated all juvenile animals. For this purpose spring juveniles were considered to be adult after November and summer juveniles after February. The weights were also separated by season in order that any fluctuation might be detected. Table 12 summarizes these data.

TABLE 12.—Seasonal Weights of Adult Fox Squirrels, 1938-1939

	Males		Females	
	No.	Weight	No.	Weight
Dec. - Feb.	64	769.8 \pm 9.83	61	778.3 \pm 10.54
Mar. - May	43	736.4 \pm 15.66	50	740.3 \pm 11.30
June - Aug.	47	744.0 \pm 12.09	62	766.6 \pm 10.78
Sept. - Nov.	44	789.7 \pm 14.52	38	802.6 \pm 13.79
Totals	198	760.8 \pm 6.40	211	770.8 \pm 5.85

Mean weight of 409 adult fox squirrels 766.0 \pm 4.33 grams. (1 lb. 11 oz.)

The average adult fox squirrel in the Allegan area during this work weighed 1 pound 11 ounces (766 g.). Males averaged 1 pound 10.8 ounces, and females 1 pound 11.2 ounces. This represents an average figure for the entire year. Weights by season are given in the table and also in Fig. 19.

It appears that in the second breeding season (summer) there is a greater difference in weight between the sexes than in the first. The winter season, with its shortage of food supplies, may well be responsible. On the average a pregnant animal is heavier than a non-pregnant one. However, it is possible that the physiological strain of bearing and nourishing a litter of young in the "lean" season of the year reduces the weight of a female enough to compensate for the expected increase in weight due to pregnancy and to the evident natural tendency of females to be slightly heavier than males.

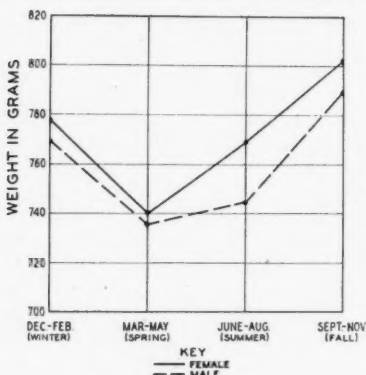


Fig. 19. Seasonal weights of adult fox squirrels. The number of animals weighed in each group and the standard error are given in table 14. Only adult squirrels were used, spring juveniles being considered adult after November and summer juveniles after February.

WEIGHT CORRELATED WITH HABITAT

The heaviest fox squirrel handled in the upland at Allegan weighed 2 pounds, 2.5 ounces. It was indeed an exceptional animal that weighed over two pounds. The acorn crop in the fall seasons of 1937 and 1938 was small and few upland animals had any conspicuous amount of fat.

On October 18, 1937, I examined a squirrel, shot by D. W. Nash, of Allegan, which scaled 2 pounds, 10 ounces. Another that was judged to be equally as large had been shot a day or so before in the same area, and a third very large individual had been seen. On October 21 Mr. Nash obtained an adult female weighing 2 pounds, 6 ounces. These squirrels had an inordinate amount of visceral and subdermal fat, and all came from a half-mile stretch of Swan Creek bottom. The creek flood-plain in this vicinity averages about 200 yards in width and supports a growth of alder, black and white ash, red maple, elm, butternut, and aspen. On the slopes are beeches and red oaks.

The yield of oak and beech mast was poor in 1937, but no doubt this creek bottom was furnishing a good supply of squirrel food. Later, in the

course of field work in this habitat, I took a male squirrel weighing 2 pounds, 4 ounces from a woodpecker hole in an aspen stub. It, too, was very fat. Squirrels taken in the oak grubs were conspicuously different, few of them showing any trace of fat either beneath the skin or in the coelum.

The respective conditions of some lowland and upland squirrels may, possibly, be a reflection of the relative fertility of the soils in the two habitats. How a plentiful food supply and good condition may affect the habits and survival of an animal is suggested by further observations made during the winter of 1937-38.

Activity

In these studies I have had no evidence of other than daylight activity among fox squirrels. They are abroad early in the morning, however, and on a bright day in winter the snow may be criss-crossed with their tracks before the sun is an hour high.

In the winter their activity appears to be conditioned by temperature and snow depth. Through a blizzard or a period of extreme cold with deep light snow they are likely to remain in the nest. Some observations from field notes will illustrate this:

On November 19, 1937, in the city of Allegan, it snowed very hard and the next day there was a foot of light powdery snow on the ground. Several times that day squirrels were seen in the trees, but there were few signs of ground activity. Under these conditions squirrels traveling between trees sometimes run for short distances beneath the surface of the snow. From the above-mentioned date until November 21 it snowed intermittently. On the 21st there was from 12 to 15 inches of snow on the level in the oak woods at the experiment station. No squirrels were observed to be active on the ground during the three days. The first tracks were seen late on the 22nd. By November 24, however, there were numerous places where squirrels had dug for acorns, and animals around the house in town were digging up walnuts.

A little snow on the ground or deep snow packed hard does not impede the activity of squirrels. With three inches of snow, on December 20, 1937, I tracked one individual for more than three-quarters of a mile from a cornfield it had visited. It had carried an ear of corn for nearly half a mile.

On December 13, in another location, four traps were placed beside the road where tracks had been plentiful. No animals were taken up to December 23, during which time there was cold weather and, until the 20th, a crust of the deep snow. On the 23rd I caught a squirrel in one of the traps. One animal was taken on December 24, one on the 25th, and three on the 26th. The next day another squirrel was trapped which repeated on the day after. This activity actually dated from the 20th, on which day the sun came out and the weather became warmer than in the week previous. At this season, of course, sexual urges are also to be considered.

On January 19, 1938, there was 8 to 12 inches of packed snow blown

smooth. One side of the squirrel woods was a maze of tracks. The animals were feeding, digging through the hard snow to get at buried acorns.

On January 28 it was 10 degrees F. below zero early in the morning. That afternoon at five o'clock it was +16 degrees. There were only four places in the squirrel woods where the animals had ventured on the ground for short distances over the 13 inches of powdery snow.

An adult female squirrel in full breeding condition was taken from a nest on January 21, 1939. There were no tracks anywhere in the vicinity on the snow that had fallen on January 18, indicating that this squirrel had probably been inactive in her nest for at least three days.

Although unpacked snow may limit movement, rain appears to be no important deterrent to activity, if the weather is warm. On November 13, 1937, it rained nearly all morning, and yet I saw a squirrel foraging in the wet grass in the midst of it. After the rain, two squirrels were active in my yard for several hours. On February 5, 1938, a squirrel crossed the road ahead of my car in a driving rain, carrying an ear of corn. On several other occasions squirrels were seen active in the rain, although it is to be doubted that they ever stay out long enough to get their fur soaked.

There are some indications that activity in winter is correlated with habitat. In the section on weight and condition, reference has been made to the very fat animals taken in Swan Creek bottom in the fall of 1937. On November 5 after the close of the hunting season 8 traps were set in the creek bottom and baited with walnuts. These traps were operated for a month without catching a squirrel. Early in December a heavy snow came, and the traps were snowed in until February 8. I made two checking trips through the area during this time and saw no squirrel tracks at all in the lowland. Along the high bank and in the upland tracks were fairly common.

There are numerous excellent den trees along Swan Creek, and I received an impression that many of the squirrels in that area were holed up during much of the cold weather. The failure to catch animals in November probably indicates that the walnuts were being passed up in favor of preferred food.

Although the evidence is poor, the strikingly greater squirrel weights in the same area where there was apparently a minimum of winter activity suggests that the relationship of the phenomena might well be that of cause and effect. It is logical, also, that a squirrel with a goodly reserve of fat would remain in safety and utilize that reserve during periods when it could forage only with difficulty. Animals without this reserve can probably remain inactive for a much shorter period. The fact that two females in or approaching oestrus are known to have been inactive during cold weather for two or three days indicates that the sexual urge may not conspicuously modify this behavior.

Summary and Conclusions

An ecological study of the western fox squirrel, *Sciurus niger rufiventer* (Geoffroy), was conducted in the extensive second-growth oak woods of Allegan County, Michigan. The region is a glacial lake bottom and is charac-

terized by its marginal to submarginal sandy soil. In primitive times it was occupied in part by the southernmost extensive stand of Michigan white pine. At present the upland supports black and white oaks, but not the hickory that is found on the glacial drift of much of the Michigan farming region. Reflecting soil conditions and the nature of the flora, the "sand plains" are, on an acreage basis, not highly productive of wildlife. The county as a whole was fifth in the state as to fox squirrel kill in the 1939 season.

The squirrel population of a 40-acre unit of woodland was studied by trapping and ear-tagging individual animals. Traps were set in a checkerboard pattern and operated in nine periods. Based upon this work, and upon field observations, it is concluded that the population of fox squirrels in the region averaged near one animal per three acres of upland oak woods during the first fall season. Evidence from the squirrel study woods, extensive observations, and the comparative numbers of squirrels caught in rabbit and raccoon traplines at the Swan Creek Wildlife Experiment Station, indicates that squirrels increased in numbers during the period of the study. This might have been due to the state-wide closed season in 1938. However, subsequent observations indicate that this species was still more numerous in 1940 after an open season in 1939, and it appears that there has been a general increase dissociated from the closed season.

The leaf nests built by fox squirrels are sufficient for their survival, since these animals regularly inhabit second-growth devoid of hollow trees. Hollows are used, however, and appear to be preferred where they are present. Although the animals may rear their young or spend the winter in either type of nest, tree cavities are probably the best protection from weather and enemies, and for this reason the preservation of hollow den trees should be an effective management technique. In locating their leaf nests fox squirrels showed a decided preference for white pine over oaks, and for black oak over white oak, in habitats where all three species occurred together.

The first breeding of this species was recorded in late December, with the greatest sexual activity coming a month later. Some breeding occurs during the spring, and there is a second rather definite period in June and July. Fox squirrels breed when ten or eleven months old. Thus, animals born in the summer do not breed until the next spring or summer, and most squirrels born in March will breed in the January or February following. Inconclusive evidence indicates that most squirrels in this region breed only once as yearlings, and that most old animals produce two litters in a season. The average number of young in litters was 2.95 in 1939.

From observations, the most important natural mortality factor was a mange-like condition which, at least in some cases, is associated with an infestation of scab mites (*Sarcoptes*). The disease causes a loss of hair, emaciation, and probably renders the animals more susceptible to exposure and predation. A small amount of predation by red-tailed hawks and dogs has been recorded, but the fox squirrel does not appear to be highly vulnerable to natural enemies. Highway mortalities among fox squirrels were conspicuous and numerous as compared with those of other species. More than half a million

squirrels are taken in the state during the hunting season, and in a species of such comparatively low fecundity this may well be the most important cause of mortality.

The year-round average weight of adult squirrels, principally from the upland oak habitat, was 766 grams, or 1 lb., 11 oz. Females averaged 10 grams heavier than males. In the yearly fluctuation squirrels were at their maximum weight in fall and the minimum in spring.

The mast crop was not large in either 1937 or 1938, and upland fox squirrels had little belly-fat. In the fall of 1937, however, in a stream-bottom habitat, squirrels were prodigiously fat in the coelum and beneath the skin of the abdomen. In this stream bottom, which contained numerous den trees, less winter activity was observed than on the upland.

This suggests that under ideal conditions food supplies will be sufficient to permit fox squirrels to become fat in the fall. With such a reserve the animals can remain inactive during periods of intense cold and deep snow. Moreover, if hollow trees are present, squirrels will have the advantage of maximum protection from weather and enemies. These considerations give some index of the environmental conditions which it will be the job of management to approximate.

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GAME DIVISION,
DEPARTMENT OF CONSERVATION,
LANSING, MICHIGAN.

The Moles (Genus *Scalopus*) of Texas

William B. Davis

In his revision of the moles, Jackson (N. Amer. Fauna, no. 38, 1915) found it necessary to leave the relationship of the moles of Texas in an uncertain status. He states (*op. cit.*, p. 51) that "local variation in the genus seems to reach its maximum in *S. a. texanus*," and he points out that many more specimens than he had available must be assembled before the group can be studied satisfactorily. In the interim of 27 years that has elapsed since Jackson made his study, additional specimens have been acquired. Although sufficient material still is not available for a comprehensive treatise, it seems timely to report upon the present state of knowledge.

Acknowledgment is due the following for the loan of material in their care: Dr. H. H. T. Jackson, Biological Survey, Collection, Washington, D. C.; Wharton Huber, Academy of Natural Sciences, Philadelphia; George C. Goodwin, American Museum of Natural History, New York; Colin C. Sanborn, Field Museum of Natural History, Chicago; F. Walter Miller, Museum of Natural History, Dallas; Edward R. Warren, Colorado Springs, Colorado; Albert J. Kirn, Somerset, Texas; Dr. J. K. G. Silvey, North Texas State Teachers College, Denton; Dr. J. C. Cross, Texas College of Arts and Industries, Kingsville; Phil D. Goodrum, Texas Game, Fish and Oyster Commission, Austin.

Abbreviations used in text to designate the collections whence specimens have been examined are as follows:

AJK—Albert J. Kirn Collection
AMNH—American Museum of Natural History
ANSP—Academy of Natural Sciences of Philadelphia
BSC—Biological Surveys Collection
DMNH—Dallas Museum of Natural History
ERW—Edward R. Warren

NTSTC—North Texas State Teachers College
TCAL—Texas College of Arts and Industries
TGFOC—Texas Game, Fish and Oyster Commission
TCWC—Texas Cooperative Wildlife Collection
USNM—United States National Museum
WBD—William B. Davis Collection

Areas of Differentiation

As judged from the 101 specimens at hand, mostly skins with skulls, five areas of differentiation of *Scalopus aquaticus* occur in Texas as follows: (1) Extreme eastern Texas, coinciding in general with the distribution of coniferous trees, (2) a small area comprising parts of Leon, Trinity, and Walker counties, (3) a larger area in east-central Texas in the sandy lands of the post oak belt, (4) the northern part of the Panhandle, and (5) the "brush country" of southern Texas (see map).

Area One.—In the extreme eastern and northeastern parts of Texas the moles are large in size and dark in color; hind foot exceeds 20 mm. in length;

skull large, more than 34 mm. in occipitonasal length, and relatively slender (ratio of mastoid breadth to occipitonasal length 50 in males); length of maxillary tooth row usually exceeds 11 mm.; maxillary breadth exceeds 10.3 mm. This population was given the subspecific name *pulcher* by Jackson in 1914.

Area Two.—Specimens from Leon, Trinity, and Walker counties are small in size and pale brownish in color; hind foot does not exceed 18 mm.; skull short, not exceeding 31 mm. in occipitonasal length, and relatively broad (ratio of mastoid breadth to occipitonasal length, 53); length of maxillary tooth row not more than 9.5 mm.; maxillary breadth less than 9.2 mm. This population has not been recognized by name.

Area Three.—The moles occupying a large area in the drainage basins of the Brazos and Colorado rivers are medium in size and hair brown in color;

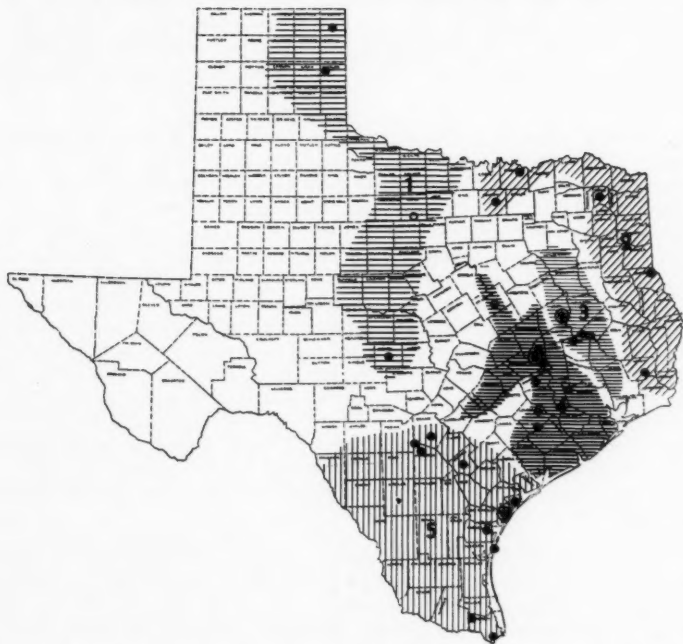


Fig. 1. Map showing the known distribution of moles in Texas: (1) *Scalopus aquaticus intermedius*, (2) *S. a. pulcher*, (3) *S. a. nanus*, (4) *S. a. cryptus*, (5) *S. a. texanus*. Solid circles indicate localities whence specimens have been examined; solid circles inside large open circles indicate type localities; small open circle indicates locality whence specimens have been reported, but not examined in the present study.

hind foot in males not less than 18 mm. nor more than 20 mm.; skull medium in size and relatively broad (ratio of mastoid breadth to occipitonasal length, 53); length of maxillary tooth row more than 10.0 mm., seldom exceeding 11 mm. (one male from Brazos County, 11.5). This population has not been recognized by name.

Area Four.—Moles from the extreme northeastern part of the Panhandle are medium in size and light in color (those examined have a silvery sheen); length of hind foot in males and females, 18-20 mm.; skull medium in size and relatively broad (ratio of mastoid breadth to occipitonasal length, 52); length of maxillary tooth row more than 10 mm., seldom exceeding 11 mm. This population was named *intermedius* by Elliot in 1899.

Area Five.—Moles in the "brush country" of southern Texas are small in size, never exceeding 150 mm. in total length (average near 135 mm.) and pale in color, often heavily suffused with copper and cinnamon on the head and under parts; length of hind foot, 15-18 mm.; skull seldom exceeding 32 mm. in occipitonasal length, shallow, and relatively broad (ratio of mastoid breadth to occipitonasal length, 53). This population was named *texanus* by Allen in 1891.

When the populations from areas 1, 2, 3, and 5, each one geographically farther to the southwest than the preceding, are lined up, the trend from the large *pulcher* in eastern Texas to the small *texanus* in southern Texas is not a gradual gradient. On the contrary, the change is abrupt from the large *pulcher* to a small animal, smaller in many respects than *texanus*, that occupies an area in Leon, Trinity, and Walker counties. This is followed by a less abrupt change to a larger animal in the Brazos and Colorado valleys, which, in turn, gives way to the small *texanus* in that part of the state south of San Antonio. Stated differently, in travelling southwestward from eastern Texas, one encounters first a population of large moles, next a population of small moles, then a population of medium-size moles, and finally the small moles of southern Texas. Because of this fact, it does not seem logical to consider the populations occupying that part of Texas between the ranges of *pulcher* and *texanus* as intergrades. Rather, it would seem that one is dealing with two populations distinct from both *pulcher* and *texanus* and at the same time recognizably different from each other. Cranial characters seem to support this view.

In spite of the distance separating the range of *intermedius* in the Panhandle and the population occupying the sandy land areas in the drainage basins of the Colorado and Brazos rivers in east central Texas and the obvious difference in the ecologic composition of the two areas, the discernible difference between them other than in color are few. Specimens from the Panhandle are paler and have slightly larger skulls.

Each of these populations is discussed below; two of them are described as new.

SCALOPUS AQUATICUS PULCHER Jackson—Arkansas Mole

Scalopus aquaticus pulcher Jackson, Proc. Biol. Soc. Washington, vol. 27, p. 19, February 2, 1914; Jackson, N. Amer. Fauna, no. 38, p. 46, September 30, 1915.

Type from Delight, Pike County, Arkansas.

Characters.—Largest and darkest of the moles in Texas; hind foot exceeds 20 mm. Skull large, occipitonasal length 34 mm. or more; ratio of mastoid breadth to occipitonasal length, 50 in males, 52 in females; length of maxillary tooth row usually exceeds 11 mm.

Distribution.—(In Texas). Extreme eastern and northeastern parts of the state, from Denton County southeastward at least to Hardin County (see map).

Remarks.—Seemingly this large mole is restricted to the sandy and loamy soils of eastern Texas in close association with the "piney woods" belt. Specimens from Denton appear to be intergrades between *pulcher* and *intermedius*; on the basis of large hind foot and dark coloration they are referred to *pulcher*.

Specimens examined.—Sixteen, as follows: Denton County: Denton, 2 (NTSTC). Grayson County: Denison, 1 (NTSTC). Titus County: Mt. Pleasant, 1 (TCAI). Shelby County: Joaquin, 1 (BSC). Hardin County: 7-9 mi. NE Sour Lake, 1 (BSC).

Scalopus aquaticus nanus n. subsp.—Dwarf mole

Type.—Female, adult, skin and skull; no. 1785, Texas Cooperative Wildlife Collection; collected June 28, 1938, 13 miles east of Centerville, Leon County, Texas, by W. C. Parker; original no. 3135 of William B. Davis.

Diagnosis.—Size small (see measurements); color pale brownish; skull small, occipitonasal length less than 31 mm. in females; maxillary tooth row short, less than 10 mm. in females; width across maxillary tooth row at alveoli less than 9 mm.

Comparisons.—As compared with *pulcher*, the geographic race immediately to the east, *nanus* differs as follows: Coloration paler, size smaller; length of maxillary tooth row in females 13 percent less (9.5 mm. as compared with 10.9 mm.); occipitonasal length in females 11 percent less (30.5 mm. as compared with 34.3 mm.). As compared with *cryptus* to the west, *nanus* differs as follows: Size smaller; length of maxillary tooth row in females 10 percent less (9.5 mm. as compared with 10.5) palatilar length less (14 mm. as compared with 15.8). As compared with *texanus* of southern Texas, *nanus* differs in darker coloration, shorter tooth row (9.5 mm. as compared with 10.0 mm. in females), and narrower maxillary width (ratio of maxillary breadth to occipitonasal length 29 as compared with 37).

Measurements.—Average and extremes (in parentheses) of three females: Total length, 140 (132-150); length of tail, 25 (21-30); length of hind foot, 17.3 (17-18); occipitonasal length, 30.6 (30.3-30.8); palatilar length, 14.1

(13.6-14.4); mastoid breadth, 16.4 (16.1-17.0); maxillary breadth, 9.0 (8.7-9.2); alveolar length of maxillary tooth row, 9.5 (9.1-9.9); depth of skull over bullae, 9.7 (9.5-9.8).

Remarks.—The only male specimen available from this area is immature. It agrees with the females in having narrow maxillary width, narrow mastoid breadth, and relatively short palatilar length.

This race, as judged by the material at hand, is well marked by small size, narrow maxillary breadth, and short maxillary tooth row.

Specimens examined.—Four, as follows: *Leon County*: 13 mi. E. Centerville, 1 (TCWC); *Walker County*: 17 mi. WNW Huntsville, 1 (TCWC). *Trinity County*: 4 mi. E. Trinity, 1 (TCWC); 7 mi. E. Trinity, 1 (TCWC).

Scalopus aquaticus cryptus n. subsp.—Central Texas Mole

Scalopus aquaticus texanus Jackson, N. Amer. Fauna, no. 38, p. 50, 1915 (part).

Type.—Male, adult, skin and skull; no. 1454, Texas Cooperative Wildlife Collection; collected November 23, 1939, at College Station, Brazos County, Texas, by U. H. Williams; original no. 8.

Diagnosis.—Size medium (see measurements); color near hair brown, with faint wash of ochraceous on head and underparts, often with silvery sheen; hind foot medium, 17-20 mm. Skull medium, occipitonasal length in adult males exceeds 33 mm., in adult females, exceeds 31.5; length of maxillary tooth row exceeds 10.2 mm. in both sexes; depth of skull seldom exceeds 10 mm.; width across maxillary tooth rows at alveoli exceeds 9 mm.

Comparisons.—As compared with *texanus*, the race geographically adjacent to the southwest, *cryptus* is larger and darker. Length of skull usually more than 32 mm., rather than less; palatilar length usually more than 15 mm., rather than less. For comparison with *nanus* to the northeast, see same. Compared with *intermedius*, to the northwest, *cryptus* differs in darker color and smaller skull. Compared with *pulcher* in eastern Texas *cryptus* is smaller in every respect except in depth of skull and maxillary breadth.

Measurements.—Average and extremes (in parentheses) of 5 adult males: Total length, 150 (143-158); length of tail, 24 (20-31); length of hind foot, 19 (18-20); occipitonasal length, 33.6 (32.9-35.7); palatilar length, 16.0 (15.6-17.3); maxillary breadth, 10.7 (10.3-11.4); mastoid breadth, 17.8 (17.2-18.5); alveolar length of maxillary tooth row, 10.9 (10.6-11.5); depth of skull over bullae, 10.0 (9.9-10.3).

Of 4 adult and subadult females: Total length, 144 (140-151); length of tail, 23 (20-27); length of hind foot, 18 (16-19); occipitonasal length, 32.2 (31.7-33.5); palatilar length, 15.1 (14.9-15.8); mastoid breadth, 16.9 (16.5-17.5); maxillary breadth, 9.9 (9.5-10.2); alveolar length of maxillary tooth row, 10.5 (10.4-10.8); depth of skull over bullae, 9.7 (9.4-10.1).

Remarks.—The range of variation in certain cranial characters (length of skull, mastoid breadth, and maxillary breadth) suggests that *cryptus* might

be nothing more than a population of intergrades between *pulcher* in eastern Texas and *texanus* in southern Texas. The relative stability of other characters (palatilar length, mastoid breadth, alveolar length of maxillary tooth row) seem to validate the naming of this population, as does the presence of a population of much smaller moles interposed between the ascribed ranges of *pulcher* and *cryptus*.

The specimen, skin and skull, from Waco is similar in most respects to the moles from College Station and Bryan except that the pelage is a light (faded?) brown. From the appearance of the fleshy parts (feet and nose) the specimen seems to have been immersed in some preservative solution before it was made into a study skin.

Specimens examined.—Nineteen, as follows: McLennan County: Waco, 1 (ANSP). Brazos County: Bryan, 4 (3, TCWC, 1, TGFOC); 3.5 mi. N Bryan, 2 (TCWC); College Station, 8 (TCWC). Washington County: Longpoint, 1 (USNM). Harris County: 2½ mi. N Hockley, 1 (TCWC). Colorado County: 6 mi. N Eagle Lake, 1 (TCWC); 20 mi. S Eagle Lake, 1 (DMNH).

SCALOPUS AQUATICUS INTERMEDIUS (Elliot)—Southern Plains Mole

Scalops machrinus intermedius Elliot, Field Columb. Mus. publ. 37, zool. series, vol. 1, p. 280, 1899.

[*Scalops*] [*aquaticus*] *intermedius* Elliot, Field Columb. Mus., publ. 45, zool. series, vol. 2, p. 390, 1901.

Scalopus aquaticus intermedius Bailey, N. Amer. Fauna, no. 25, p. 207, 1905; Jackson, N. Amer. Fauna, no. 38, p. 49, 1915.

Scalopus aquaticus texanus Jackson, N. Amer. Fauna, no. 38, p. 50, 1915 (part).

Type from Alva, Woods County, Oklahoma.

Character.—Size medium; color pale, often with silvery sheen, with suffusion of ochraceous on nose and wrists; underparts silvery plumbeous, faintly washed with ochraceous. Length of hind foot, 18-20 mm. Occipitonasal length usually more than 33 mm.; length of maxillary tooth row exceeds 10.5 mm.

Distribution (in Texas).—Extreme northern part of the Panhandle, south as far as Mason County (see map).

Remarks.—Jackson (N. Amer. Fauna, no. 38, p. 52, 1915) referred the three specimens from Mason to *texanus* on the basis of narrow rostra and flat skulls, although pointing out that they approached *intermedius* in large size and pale coloration. I have examined these specimens and in my opinion they are best referred to *intermedius*. In five characters, namely, length of skull, palatilar length, mastoid breadth, maxillary breadth, and pale color, they are far above the average of *texanus* and agree with *intermedius*; in two characters, flattened skull, and short maxillary tooth row, they agree with *texanus*. With respect to the width of the rostrum (measured across the canines), they equal *intermedius* and exceed *texanus*.

Specimens examined.—Eight, as follows: Lipscomb County: Lipscomb, 3 (BSC). Wheeler County: Mobeetie, 2 (BSC). Mason County: Mason, 3 (USNM). Additional record: Young County: Belknap (Jackson, 1915).

SCALOPUS AQUATICUS TEXANUS (Allen)—South Texas Mole

Scalops argentatus texanus Allen, Bull. Amer. Mus. Nat. Hist., vol. 3, p. 221, April 29, 1891.

Scalops texanus Allen, Bull. Amer. Mus. Nat. Hist., vol. 5, p. 200, 1893.

Scalops aquaticus texanus True, Proc. U. S. Nat. Mus., vol. 19, p. 21, 1896.

[*Scalops*] [*quaticus*] *texensis* (sic). Elliot, Field Columb. Mus., publ. 45, zool. series, vol. 2, p. 390, 1901.

Scalopus aquaticus texanus Bailey, N. Amer. Fauna, no. 25, p. 206, 1905.

Scalopus aquaticus texensis (sic.) Elliot, Field Columb. Mus., publ. 105, zool. series, vol. 6, p. 471, 1905.

Scalopus aquaticus texanus Jackson, N. Amer. Fauna, no. 38, p. 50, 1915.

Type from Rockport, Aransas County, Texas.

Characters.—Except for *nanus*, smallest of the moles in Texas; length of hind foot seldom more than 19 mm.; total length seldom more than 140 mm. Skull small and flat, seldom exceeding 33 mm. in occipitonasal length and seldom equalling 10 mm. in depth; maxillary breadth usually less than 10 mm.; alveolar length of maxillary tooth row seldom more than 10.5 mm.

Distribution.—Southern Texas, south of the Balcones Escarpment; north to San Antonio and east at least to Austwell (see map).

Remarks.—This race, as here restricted appears to be fairly uniform in character; specimens from San Antonio average slightly larger than specimens from Rockport, but in most respects they fall within the range of individual variation of the Rockport series. Slight variations also are evident in specimens from Padre Island, Santa Rosa, and Brownsville, but in most instances they fall within the range of individual variation found in the Rockport series.

Specimens examined.—Fifty-four, as follows: *Bexar County*: San Antonio, 3 (AMNH). *Atascosa County*: 7 mi. SW Somerset, 19 (AJK); Benton, 1 (AJK). *Karnes County*: Kennedy, 1 (TCAI). *Aransas County*: Rockport, 22 (17, AMNH; 2, BSC; 1, FMNH; 2, ERW); Aransas National Wildlife Refuge, 1 (TCWC). *Nueces County*: Corpus Christi, 1 (BSC); Padre Island, 3 (2, BSC; 1, USNM). *Cameron County*: Brownsville, 2 (USNM); Santa Rosa, 1 (BSC).

TEXAS COOPERATIVE WILDLIFE RESEARCH UNIT,
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The Biology of the Least Shrew-Mole, *Neurotrichus gibbsii minor*

Walter W. Dalquest and Donald R. Orcutt

The life history and economic status of four of the five genera of North American moles have been studied extensively by a number of workers, and literature on the subjects is voluminous. The genus *Neurotrichus*, however, the smallest and least fossorial of the American Talpidae, has been almost totally neglected in this respect. We find but four papers dealing with the habits of the shrew-mole: a short paper by Race¹ (1929), and several paragraphs in general works by Jackson (1915), Taylor and Shaw (1927), and by Bailey (1936). The present report serves to expand the knowledge of the biology of American moles and to place on record a number of unreported facts about *Neurotrichus*.

Methods

Observations of the life history of *Neurotrichus* were begun by the senior author in 1936 and continued intermittently for five years. Mr. Robert L. Burgner assisted in the work for several months in 1940. The junior author began work on the problem in 1940. Studies were carried on most actively in the months from February to June; less actively from October to November and but incidentally in December and January. No work was done between June and October, except for a few observations made in the summer of 1940.

Data pertinent to the present problem were obtained by field observations, trapping records, laboratory examinations, and experiments on captive animals. We are deeply indebted to Professor Trevor Kincaid, University of Washington Department of Zoology, and to Dr. Victor B. Scheffer, U. S. Fish and Wildlife Service, whose kindness and cooperation have made this work possible. We wish to thank also Dr. William J. Hamilton, Jr., Cornell University, for critically reading the manuscript. Mr. Robert L. Burgner turned over to us his field notes to use as we wished. Mrs. Martha R. Flahaut, Washington State Museum, allowed us full use of the specimens in her care. Dr. R. W. Kenworthy, University of Washington Department of Physics, furnished valuable aid in certain experiments.

Distribution

The genus *Neurotrichus*, with its single species, *gibbsii*, is found in the humid Pacific Coastal Belt from southern British Columbia south, through and west of the Cascade-Sierra Nevada Mountains, into California. Three subspecies are recognized: *hyacinthinus* in California, *gibbsii* in the Cascade

Mountains, and *minor* in the lowlands of western Washington (Fig. 1). The present paper deals entirely with the race *minor*.

Identification

Neurotrichus gibbsii minor is the smallest known race of its genus, and is the smallest American mole. In total length it is actually exceeded by the shrews with which it is found associated. Average and extreme measurements, in millimeters, of 85 adult specimens are: total length, 107.0 (100-117); length of tail, 35.3 (31-39); length of hind foot, 15.0 (14-16). There is little variation in weight; 30 specimens average 10 grams (9.5-10.5). No differences in measurements or weights could be found between male and female shrew-moles.

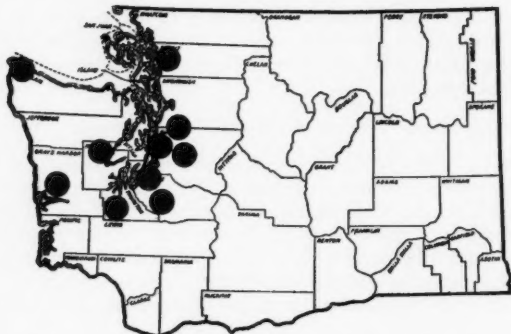


Fig. 1. Distribution of *Neurotrichus gibbsii minor*. Records from published and private sources.

The shrew-mole is well named, for in appearance it is half-way between a mole and a shrew (Fig. 2). It possesses the large head and heavy dentition of a mole combined with a coat composed of both guard hair and underfur directed posteriorly, as in a shrew. The forelegs appear relatively long as compared with *Scapanus*. The forefeet and pectoral region are specialized for digging, but are not as specialized as those of *Parascalops*. The forefeet of *Neurotrichus* are longer (to base of claws) than wide, while in *Scapanus* the reverse is true. The radius and ulna of *Neurotrichus* are relatively longer and thinner than those of *Parascalops*. The humerus and clavicle of *Neurotrichus* are relatively thin and round, not flat and massive, as compared with *Parascalops*. The thick, hairy, constricted tail resembles that of *Parascalops*.

The fur of *Neurotrichus* is sooty blue-black in color. The guard hairs give the upper parts a rough appearance, but the under-parts are sleek. The tail and feet are markedly scaled. The backs of the feet are almost violet in color while the soles are pink. The tail is short, thick, constricted at the base, and save for the basal 5 mm., covered with short, stiff, black hairs about 2.5

mm. long. The tip of the tail is blunt and possesses a tuft of hairs 4.4 mm. long.

The eyes of *Neurotrichus* are tiny and concealed in the fur. The nose is elongate and flattened dorso-ventrally. Its width at the incisors is 4 mm. while its depth at the same place is 2 mm. The nose extends 8 mm. past the incisors and the terminus is flared to form a pad 2 mm. wide. In life, for 2 mm. at the tip, the nose is deep pink in color and usually damp. The nostrils are placed laterally. The auditory orifice of the shrew-mole is an oval slit 4 x 2 mm. in extent.

The nose of *Neurotrichus* possesses 8 pairs of vibrissae, about 5 mm. anterior to the eyes. The latter vary from 6 to 12 mm. in length. There are 2 pairs of vibrissae about 11 mm. long situated on the sides of the head about 5 mm. anterior to the ears. There is also a fringe of short bristles about 0.5 mm. long on the sides of the terminal 5 mm. of the nose.

The palm of the forefoot of *Neurotrichus* measures 4 x 5.4 mm. (to base of claws), while its greatest depth is 2 mm. The foreclaws of the least shrew-mole are long and curved. The ventral surfaces of the claws are beveled, with the long, sharp edges next to the body, except in the outermost claw where the reverse is true.

Habitat

The entire northern half of the western part of the State of Washington is mantled by a thick layer of glacial debris, deposited by the continental glaciers of Pleistocene times. The resultant rolling topography was, before the coming of the white man, clothed with dense Douglas fir, western hemlock, and red cedar forest. Because the giant trees overhead so completely blocked the light, only the most shade tolerant of underbrush was able to survive beneath the forest. The forest floor habitat supported a typical fauna, in which insectivorous mammals were unimportant.

Along rivers and streams, however, deciduous vegetation grew in abundance. Thick tangles of alder, maples, various bushes, and vines defied penetration and formed the habitat of many moles and shrews. With the coming of the white man the coniferous forests were cleared, but the impenetrable ravines and gullies were of no economic importance. These still exist, even in some otherwise thickly populated regions.

Several such ravines are situated on the University of Washington Campus, surrounded by miles of city blocks, business districts, and human habitations. In these ravines we studied *Neurotrichus* (Dalquest and Burgner, 1941).

The ravines where the present work was carried on are situated on the eastern side of the campus. They are three in number, of which the southern two were most extensively used. The ravines are deeply cut in hard glacial till. Landsliding has modified their heads to a blunt 'U' shape and steepened their sides to a 35 degree slope. The ravines previously opened to Lake Washington, on the east, but a highway and railroad embankment now effectively close the mouths.

Numerous tiny springs emerge at the heads and along the sides of the ravines. These form tiny streamlets which wind back and forth on the ravine floors, disappearing here and there in muddy areas or *Aplodontia* burrows, to emerge at other places, and finally coalesce at the ravine mouths to form single streams. The depth of the water table of the ravine varies from place to place. At its deepest it is less than a foot beneath the surface, and in most places a footprint quickly fills with water.

The soil of the ravine is black silt. Its depth varies greatly but in most places is over a foot. Beneath the silt is compact glacial till. The soil is soft and damp at all times. Its humus content is very high. The moisture content of average samples was found to vary from 65% to 85% by weight. Ignition of dry soil samples resulted in a loss of 16% to 61% by weight, through removal of humus.

A few large red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) trees occur in the ravines, widely scattered. The dominant trees are maples (*Acer macrophyllum* and *A. circinatum*), alder (*Alnus oregona*), and flowering dogwood (*Cornus nuttallii*). Beneath the trees is a thick jungle of red elderberry (*Sambucus callicarpa*), salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), and Devil's club (*Fatsia horrida*), laced together with trailing blackberry (*Rubus ursinus*). Sword ferns (*Polystichum munitum*), mosses, and various annuals are found beneath the underbrush. Where pools of water or mud occur, the skunk cabbage (*Lysichiton americanum*) is found.

The ravine floor is littered with rotting logs and stumps. The soil is covered with a layer of dead leaves and twigs. Beneath the surface layer of moss and decaying vegetation, the trails of *Neurotrichus* form a close network of intersecting tunnels and runways.

Ranking second, to the ravine habitat in comparative abundance of *Neurotrichus*, is the lake-shore swamp habitat. This habitat includes cat-tail marshes, grassy meadows, and willow thickets. The willow thickets are often quite extensive around the shores of the glacier-formed lakes of western Washington. The thickets are dense; the soil is soft, damp silt covered with a layer of dead leaves and twigs; the water table is but an inch or two beneath the surface; and conditions are essentially the same as those in the ravines. *Neurotrichus* is sometimes reasonably numerous in such thickets, but not as abundant as in ravines. We have never taken *Neurotrichus* in cattail marshes or meadows. Presumably sod-covered surfaces offer difficult burrowing to shrew-moles.

A third habitat where we have taken *Neurotrichus* is logged-off land. This differs from the above habitats in that the soil is dry, stony, and hard. *Neurotrichus* is very scarce in such places.

General Habits

Activity.—The least shrew-mole is as diurnal as it is nocturnal. About as many specimens were trapped by day as were trapped by night. We did not

find them to be more active at any particular hour of the day or night. It is likely that activity is related to food conditions, for captive specimens usually rested or slept following a heavy meal. Individuals were apt to be found sleeping at almost any hour of the day or night.

Movements.—The ordinary movements of *Neurotrichus* on the surface of the ground consist of a slow walk, a scuttling rush, and momentary pauses. *Neurotrichus* is able to move about on the surface with considerable grace and agility, not at all like the clumsy *Scapanus*. In walking, the claws of the forefeet are bent inwards and the animal actually walks on the backs of the foreclaws.

When hunting food, most movements are accompanied by activity of the prehensile nose. This may be thrown high in the air, twisted to one side or the other, rapped on the ground, or hooked under the body. Rapping the nose on a surface seems characteristic of the shrew-mole. In an ordinary search for food the nose is rapped first on the ground directly in front of the animal. The head is then swung 40 degrees to the right and the ground is lightly rapped again. The head is then swung to the left side and a third rap given. The animal then moves one step forward. These raps follow each other with extreme rapidity. A tapping sound often serves to locate a shrew-mole when it is hunting for food in dead leaves.

Periods of activity are followed by "rest periods." These apparently are devoted primarily to the digestion of food, but not entirely so. Rest periods vary from one to eight minutes in length and occur at irregular intervals from two to eighteen minutes apart. The more food an animal eats, the longer and more frequent are its rest periods. Shorter rest periods occur at greater time intervals when an animal is unsuccessfully searching for food.

During rest periods an animal's respiration becomes slower, its nose is relaxed and usually lies flat against the ground, and its attitude is one of relaxation. Rest periods are occasionally interrupted when an animal elevates its nose for a few half-hearted sniffs or scratches vigorously with fore or hind feet.

When frightened, *Neurotrichus* makes an unbelievably swift, scuttling dash for cover. Once under a leaf or stone it crouches absolutely still, save for the rapid heaving of its sides. The animal, regardless of how badly frightened it is, soon forgets its fear, and after a minute or less reappears and resumes its restless hunting.

Climbing.—We found, to our surprise, that *Neurotrichus* is an active and agile climber. It swiftly climbs a person's hand, a twig, or the sides of a wire cage. A twig of fresh willow was stuck in the sand floor of an aquarium housing a *Neurotrichus*. As soon as the animal discovered the twig it proceeded to climb, investigating the under side of each leaf in search of insects. We received a distinct impression that this was a habit of the animal and suspect that shrew-moles in the wild often climb low bushes in search of food.

The movements of *Neurotrichus* when climbing are very deliberate. Speci-

mens always descended tail first and never took a step, up or down, until the feet were solidly placed. Under no circumstances were any of our specimens seen to jump.

Howell (1923) found *Scapanus* unable to rise to its hind legs unless its forefeet were supported. We found *Neurotrichus* often stretched up on its hind feet without support for the front feet (Fig. 2).

Swimming.—We trapped several *Neurotrichus* on a tiny island, in a small, swift-flowing stream, which they could have reached only by swimming. We tested the swimming power of *Neurotrichus* by placing a specimen in a large aquarium full of water. The results were astonishing! The animal simply flew through the water with powerful movements of all four feet. The forward motion was so great that the head and fully two-thirds of the body were above water. *Neurotrichus* uses the feet on each side of the body alternately in swimming, giving an undulating motion to body and tail.

Sleeping.—The shrew-mole sleeps curled up, with the head down between the forelegs. The weight of the body is borne by the top of the head and the hindquarters. This same position has been described by Howell (1923) for *Scapanus*.

Burrows and Burrowing.—The burrows of *Neurotrichus* were described by Racey (1929). Those excavated by us were of two types: runways and deep burrows.

Runways can be found in any good *Neurotrichus* locality by pulling away the surface cover of dead vegetation. The runways are essentially shallow troughs, one and one-half inches wide and three-quarters of an inch deep, which form a complex, interlocking network. These runways seem to be constructed in search of food and may be traveled regularly to obtain earthworms and isopods which climb or fall from the roofing cover of vegetation.

The true burrows of *Neurotrichus* are less abundant than the runways. The burrows are narrow, about an inch or less in diameter, and seldom descend as deep as one foot beneath the surface of the ground. The burrows branch, intersect, and cross each other at different levels. *Neurotrichus* burrows resemble the burrows of other moles save that they are less extensive, have open entrances, and often contain an enlarged chamber just at the water table. This "water table chamber" measures about five inches in diameter and possesses an arched roof about three inches high. The chamber is always placed at such a depth that the floor is soft, level mud. We are unable to account for this chamber or its use.

Racey (1929) was puzzled by certain tiny openings, too small to admit a shrew-mole, which often occur in the roofs of shallow burrows. We found that the burrows immediately below these openings were often slightly enlarged in the form of a small chamber. Observations of captive specimens disclosed the use of these openings. They are simply ventilation ducts for an animal asleep directly below. Shrew-moles placed in an aquarium full of sand constructed these openings in the roofs of shallow burrows. With the aid of a

flashlight we were usually able to find animals asleep beneath the openings.

The actions of *Neurotrichus* while digging are essentially the same as those of *Scalopus* (described by Hisaw, 1923b). Earth is pushed aside by lateral motions of the forefeet. The body is rotated at a 45 degree angle, and only one foot is used at a time. As far as we could discover *Neurotrichus* does not make "mole hills," but forms a burrow by pressing aside and packing loose, damp earth.

Social Habits.—Shrew-moles seem to be quite gregarious. They apparently travel in loose bands, for a line of traps set along a log or stump will catch no specimens for several days or weeks, then take several *Neurotrichus* in succession. A band of *Neurotrichus* may invade an area and remain there for from several hours to several days. Whether the band is trapped out in this time or whether it then moves on we could not determine.

Marking and releasing captured *Neurotrichus* proved impractical, for our live traps held too few living animals. Most of our specimens were taken dead in snap traps. We were therefore unable to determine the size of a band or its rate of movement. Our greatest catch of *Neurotrichus* in one place in one day included 11 individuals, taken in a line of traps set along a log 50 feet in length. No *Neurotrichus* had been taken in these traps for four days previous to this catch. In this case, at least, a band contained 11 or more individuals.

Because of the wandering habits and the impossibility of live trapping and marking any considerable number of *Neurotrichus*, we were unable to discover the extent of the range of an individual shrew-mole. The actual concentration of shrew-moles in any area varies with food conditions, etc. Under natural conditions in a favorable habitat, such as the ravines studied, we believe the normal population averages about 5 or 6 animals to the acre. In trapping specimens of *Neurotrichus*, specimens of other small mammals are also caught. This automatically changes the normal balance of small mammals in the ravine. Under such artificial conditions as the absolute removal of all other small mammals, population densities of as high as 100 *Neurotrichus* to the acre were achieved.

Food Habits

Probably 99 percent of a shrew-mole's active life is spent in a ceaseless quest for food. Captive specimens, newly placed in their living quarters, totally forgot their recent experiences and within a few moments were restlessly tapping their noses, turning over leaves, investigating crevices, or otherwise hunting for food. This is easily understood when one realizes that the shrew-mole's greatest enemy is its own appetite. A healthy, well-fed individual starves to death if left without food for a few hours!

Racey (1929) reported that shrew-moles taken in live traps died of shock. Over 90 percent of the shrew-moles taken by us in live traps were also found dead, not of shock, but of starvation, as we determined by dissection. We

believe that starvation is the cause of the death of many of the shrew-moles which are often found dead along trails and streams.

A healthy, well-fed *Neurotrichus* was left without food and observed at intervals. Six hours later the specimen seemed to become dizzy and occasionally stumbled. One hour later spells of trembling were noted. These became increasingly violent. The animal's hindquarters became paralyzed. The hind legs stiffened, straightened, and were drawn forward. The animal remained in one position until, in a violent trembling spell, it fell on its side. Attempts to administer food failed and, 11 hours after all food had been removed from the cage, the animal died.

The actions of moles while eating earthworms have been described by several writers. Howell (1923) found that *Scapanus* crushed a worm by biting it from end to end, then started to eat the worm at one end, stripping the worm between the forefeet as it ate to remove earth from the surface and mud from the intestine. Hanawalt (1922) found that *Scalopus* sometimes pulled large worms to pieces. Hisaw (1923a) reported that *Scalopus* sometimes stripped worms through the claws and sometimes did not, and began to eat a worm from either end or the middle.

Different shrew-moles handled earthworms differently. Some stripped them through the forefeet while some did not. Some bit worms along their entire length and others merely bit the worm from the portion first encountered to the nearest end. Most shrew-moles began to eat at one end of a worm, but one specimen always cut a worm into small pieces which were eaten at leisure. One shrew-mole would bite small pieces from the tail of a living worm, chew and swallow the pieces, then pursue and drag forth the maimed creature for another bite. Injured worms often escaped from this animal.

Insect pupae and isopods encountered by *Neurotrichus* were "hooked" with the nose and given a quick jerk backward to place them off balance. These were then pounced upon and eaten completely. Insects or bits of fresh meat were usually struck repeated blows with the forefeet or covered with earth or sand.

One captive *Neurotrichus* would eat only earthworms, isopods, and insect pupae. Another would eat or try to eat almost anything offered. Dead mice and amphibians were usually eaten by shrew-moles if other food was lacking. Live frogs and salamanders were never molested. Live snails were usually investigated and half-heartedly nibbled. Smashed snails were quickly eaten. Soft-bodied insects, such as cockroaches, were eaten. Rolled oats and peanut butter were eaten in small quantities. Beetles, ants, myriapods, terrestrial mites, and slugs were refused.

The stomachs of 39 *Neurotrichus* specimens, collected in damp ravines near Seattle in the spring months of 1940 and 1941, were examined. The contents were finely chewed and very difficult to identify, but the approximate percentages by bulk were obtained. No satisfactory way to distinguish between various kinds of insect pupae was found.

TABLE 1.—Stomach Contents of 39 Shrew-moles Collected near Seattle, Spring Months, 1940 and 1941.

Food	Percent by volume	Number of Stomachs
Earthworms	42	39
Isopods	36	39
Insect larvae and pupae	12	36
Springtails	2	28
Unidentified	8	38

The quantity of food eaten by *Neurotrichus* is enormous. A *Neurotrichus* weighing 10 grams ate a worm weighing 1.26 grams in 10 minutes. One specimen ate 4.7 grams of worms in two hours. The greatest quantity of food eaten by one shrew-mole in 12 hours was 14.4 grams, or 1.4 times the animal's weight.

The scats of *Neurotrichus* are about 4 mm. long and 1 mm. wide. They are black in color, usually shiny with bits of cuticle or chitin. They are soft and disintegrate rapidly. Feces and urine are evacuated wherever the animal happens to be. No attempt at sanitary disposal of waste material was shown, and shrew-moles often dragged their tails through their own feces.

Breeding Habits

The sex of 100 *Neurotrichus* specimens was carefully determined. The series was found to include 46 males and 54 females.

The breeding season of *Neurotrichus* is very long. A male in breeding condition was taken as early as February 23, 1937, and two nursing females as late as September 26, 1939. Breeding records after the second week in May, however, are unusual. Over 80 percent of our records come between March 10 and May 14. Even in this period nearly 95 percent of the specimens taken were non-breeding.

Pregnant shrew-moles are rarely taken. We have found but 5 pregnant animals out of several hundred specimens trapped. Of these five specimens, one contained one embryo, two contained 3 embryos, one contained 4 embryos, and one gave birth to 3 young while in captivity. A nest containing 3 small shrew-moles was found. Racey (1929) reported a specimen of *Neurotrichus gibbsii gibbsii* with 4 embryos.

The gestation period of *Neurotrichus* is not known. It is greater than 15 days, however, for a specimen caught February 20, 1941, gave birth to 3 young on March 7. Unfortunately the birth of these young coincided exactly with a national defense "blackout" of the city of Seattle. Parturition took place with the adult partially concealed in a burrow. We were able to see a few details with the aid of matches. The head of the adult was bent down, between the forelegs, the hind legs were widely straddled, and the tail was held vertical.

When the blackout ended and normal light was resumed, one of the young was found alive, half buried in the sand. The other two were found mangled and dead, killed accidentally or purposely by the mother. The survivor at one hour of age (Fig. 3) measured: total length 26 mm., tail 5 mm.,

hind foot 3.6 mm., and weight 0.67 grams. The body was dull pink in color. The eyes appeared as tiny black dots. The mouth was open. The spade-like shape of the forefeet was already apparent. The animal squirmed much and kicked with all four feet. The mother refused to nurse the baby, which was found dead the following morning.



Fig. 2. Least shrew-mole, *Neurotrichus gibbsii minor*; adult female captured at Seattle, Washington, September 14, 1939; natural size. (U. S. Fish and Wildlife Service, Field Photo No. 719).

On March 24, 1941, we discovered the nest of a shrew-mole near Lake Washington, Seattle. The nest consisted of a handful of *damp* willow leaves placed two feet above the ground in an old, rotten, alder stump. The nest was reached by the mole through a burrow constructed in the interior of the stump. Three young of unknown age were found in the nest (Fig. 4). These measured respectively: total length 80, 77, 79 mm., tail 25, 24.5, 25.5 mm., hind foot 13, 13, 12 mm., and weight 6.2, 6.3, and 6.0 grams. Their eyes were closed and the auditory orifice was represented by a shallow trench. The animals attempted to bite, although their teeth had not yet erupted. The color of the skin and fur of the upper parts was dark, bluish black. The fur was soft and downlike. The fur was especially short on the under-parts, where its color was almost silver-grey. The feet and nose were pink. The skin of the anal region was much folded. The tail was relatively long, thick, and of a bluish-violet color. The forefeet were turned out, with the palms away from the body.

Physiology

Touch.—Touch seems to be the most highly developed sense possessed by *Neurotrichus*. The long, prehensile nose serves as a blind man's cane to guide the animal through life. The shrew-mole's sense of touch serves to identify in a moment any object encountered by the soft nose-pad. The gentlest contact of a single barbule of a feather on nose, face, or vibrissae receives immediate response. When a bit of blood and hair adhered to the vibrissae of one *Neurotrichus*, the animal became almost frantic in its efforts to remove the material with its front feet. The stiff hairs which rim the ears are extreme-

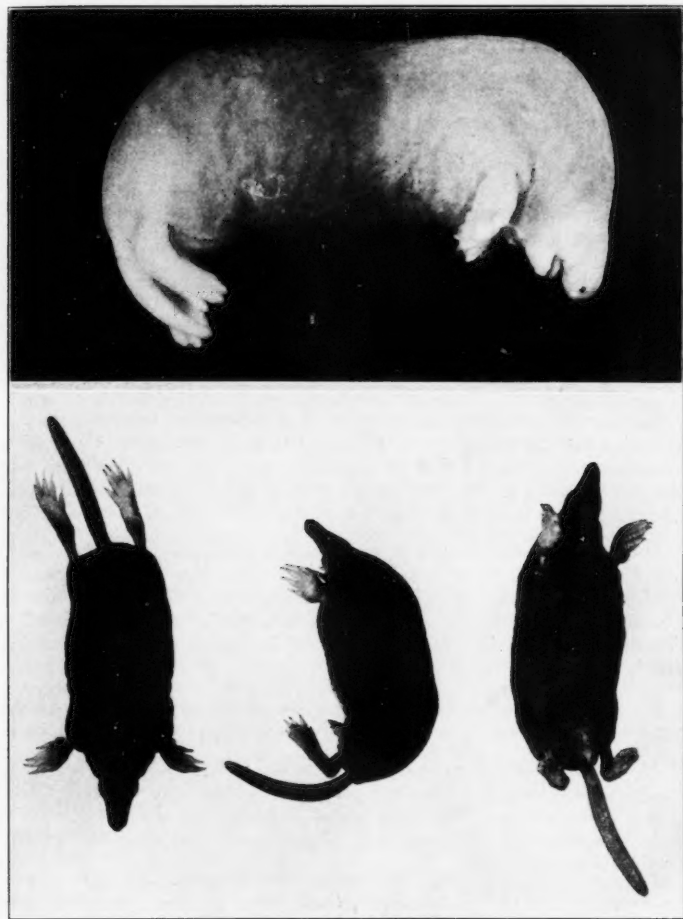


Fig. 3. (Upper). Least shrew-mole one hour old, one of a litter of three born in captivity March 7, 1941, from a pregnant female captured at Seattle, Washington, February 20, 1941; 6 \times natural size.

Fig. 4. (Lower). Litter of least shrew-moles approximately three-fourths grown, removed from a nest in a rotten stump, Seattle, Washington, March 24, 1941; 0.75 natural size.

ly sensitive. The bristles of the tail may be tactile, but are less acutely so than the vibrissae.

How sensitive a shrew-mole is to ground vibrations we could not determine. An insect or lead shot dropped in the vicinity of a captive animal usually caused it to jump or start. Both the sense of touch and hearing may play a part, however, in this reaction.

Hearing.—We noted that *Neurotrichus* did not respond to the sound of an ordinary pitched human voice, but a high-pitched squeak caused them to start or run for shelter. We attempted to test the range of hearing in the shrew-mole with a beat frequency oscillator capable of emitting notes as high as 40,000 vibrations per second. The results were not too satisfactory for it proved difficult to tell when the animal was responding to the sound. Apparent response was noted between 8,000 and 30,000 vibrations per second. Our own hearing under the same conditions ranged from under 1,000 to over 17,000 vibrations per second. Apparently the hearing of *Neurotrichus* is adapted to very high-pitched sounds, such as those made by insects.

Smell.—The constantly active nose of *Neurotrichus* first gave us the impression that the animal's sense of smell was highly developed. Close observation, however, indicated that the sense of smell in the shrew-mole was very poorly developed and of little or no use in locating food or enemies. The nose is a tactile organ and not until an object is actually touched is it discovered.

Shrew-moles often missed a motionless bit of food, though the nose might have passed within a few millimeters of it. One *Neurotrichus* repeatedly blundered into a frog, though each contact caused it to dash for shelter. Whenever a living invertebrate was encountered, i.e., actually touched, a *Neurotrichus* started in surprise. Never did its actions indicate that it had been forewarned by a sense of smell.

Shrew-moles, especially breeding males, give off a musky odor. It is possible that the sense of smell in *Neurotrichus* is specialized to detect certain odors.

Sight.—The least shrew-mole is absolutely blind. Specimens placed in almost absolute darkness made no response to a brilliant light suddenly flashed an inch from their eyes. Specimens placed in bright light did not respond to shadows suddenly passed over them. Their behavior at all times indicated complete absence of sight.

Voice.—As far as we could tell, *Neurotrichus* is mute. We never heard one make a vocal sound of any description, even very young animals or fighting males. Considering the high range of hearing in *Neurotrichus*, however, it seems likely that they may emit a note too highly pitched for human ears.

Respiration.—The rate of respiration in *Neurotrichus*, measured in rest periods, was found to average 3.4 breaths per second. Respiration is somewhat slower than this when animals are asleep, and considerably faster in activity periods.

Speed of Digestion.—The speed of digestion in the least shrew-mole, i.e., the time elapsing between the eating of food and the appearance of the same food in the fecal material, varies somewhat with the type of food eaten. When an animal whose stomach and intestines were filled with flesh was fed earthworms or isopods, chitin or setae usually appeared in the fecal material about 35 minutes later. When a shrew-mole whose diet for 24 hours previously had consisted entirely of earthworms or isopods was fed flesh, the flesh could usually be detected in feces defecated 40 minutes later.

Water Consumption.—In the early part of this study, dishes of water were kept in the cages of captive shrew-moles. Only one animal was seen to drink from a dish. Unavailability of water seemed not to effect the health of the animals. The soil of the cages was moist, but not wet. Probably the shrew-mole is able to obtain from the bodies of its prey sufficient water to make actual drinking unnecessary.

Strength.—Jackson (1922) reported that a specimen of *Scalopus* was able to move a ten pound weight. Arlton (1936) remarked on the strength of moles in forcing up sod, and devised an apparatus for use in testing the strength of *Scalopus*. One specimen so tested moved a mass of 32 times its own weight.

A modification of Arlton's apparatus was used in testing the strength of *Neurotrichus*. The greatest weight lifted vertically was 209 grams; 20 times the animal's weight. Though relatively less powerful than *Scalopus*, *Neurotrichus* is still an astonishingly strong animal.

Hardiness.—Captive specimens required a constant supply of fresh food but otherwise were not difficult to keep alive. They showed great resistance to environmental changes. Specimens were kept with equal success in aquaria filled with sand or earth, moist or dry, and in open wire cages. Temperature variations of from 45 to 80 degrees F. did not affect them. Repeated handling and use in experiments did not seem to bother them. One specimen squirmed out of a hand and fell five feet to a cement floor without suffering any noticeable ill effects. None of our captive specimens died from a cause other than starvation. We found *Neurotrichus* to be a very hardy animal, not at all susceptible to shock.

Parasites and Enemies

The commonest ectoparasite found on *Neurotrichus* is a small mite. About one specimen in ten is parasitized by an unidentified flea. Rarely a large tick (*Ixodes* sp.) is found on the head or neck of a shrew-mole. Endoparasites are rare and consist of a microscopic, unidentified roundworm of the large intestine and a large tapeworm (*Hymenolepis* sp.) in the small intestine. Numerous shrew-moles were dissected but no tumors, infections, or pathologic tissues were noted.

The blind, blundering *Neurotrichus* makes an easy prey for almost any predator. We have records of *Neurotrichus* being found in the stomachs of:

two garter snakes (*Thamnophis o. ordinoides*), a red-tailed hawk (*Buteo borealis calurus*), and a raccoon (*Procyon lotor pacifica*). Examination of pellets regurgitated by the Kennicott screech owl (*Otis asio kennicotti*) on the University of Washington campus showed that *Neurotrichus* constituted 5% of the mammals eaten by this bird in the winter. J. C. von Bloeker (1937) found remains of 2 *Neurotrichus gibbsii hyacinthinus* in owl (*Tyto* ?) pellets in San Benito County, California. Seemingly owls are the shrew-mole's worst enemy, though garter snakes, weasels, and house cats probably kill many.

Vertebrate Associations

The damp ravines where *Neurotrichus* is most common usually abound in other vertebrates. The commonest mammals in such areas are: the lowland deer-mouse (*Peromyscus maniculatus austerus*), the wandering shrew (*Sorex vagrans vagrans*), and the Trowbridge shrew (*Sorex trowbridgii trowbridgii*). The ecologic relationship of these three mammals to *Neurotrichus* has been discussed in an earlier paper (Dalquest, 1941). Under normal conditions the populations of each of these three species outnumber the *Neurotrichus* population. Apparently these mammals compete extensively with *Neurotrichus* for the available food supply, for with the removal of any or all of these forms the *Neurotrichus* population increases.

The exact ecologic relationship of the mountain beaver (*Aplodontia rufa rufa*) to *Neurotrichus* was not worked out. These clumsy mammals are vegetarians and do not compete with or prey on *Neurotrichus*. The burrows of *Aplodontia*, six inches or more in diameter, invariably occur where *Neurotrichus* are found. The burrows of *Aplodontia* extend down to the water table in even very dry places, and supply water as well as shelter to many small mammals of the Pacific Northwest. The benevolent ecologic relationships of *Aplodontia* offer a fertile field for research.

Neurotrichus generally prefers a damper habitat than the coast mole (*Scapanus orarius*) or the Townsend mole (*Scapanus townsendii*), but occasionally all three are found in the same area. On some occasions we found the burrows of the larger moles intersecting and destroying *Neurotrichus* runways. Seemingly the larger moles compete with *Neurotrichus*.

Jumping mice (*Zapus trinotatus*), creeping mice (*Microtus oregoni*), salamanders (*Ensatina*, *Ambystoma*, *Plethodon*, *Triturus*), and frogs (*Rana*, *Hyla*) have been trapped in *Neurotrichus* runways and probably compete to some extent with *Neurotrichus* for the food supply.

Economic Status

The localities where *Neurotrichus* occurs are usually unsuited to agriculture. The earthworms and isopods which constitute the principal food of the shrew-mole are of no great importance to man. The timber of the damp ravines, except the red cedar, is of little value, and hence the destruction of bark beetles and other injurious insects is of but slight benefit. The scarcity

and small size of *Neurotrichus* makes it unimportant as food for fur-bearing mammals. When everything is considered, the economic status of the least shrew-mole must be very nearly zero. The shrew-mole is, however, a unique and interesting form of life and its very existence adds much to the enchantment of the great rain forests of the Northwest.

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The Parasites, Predators, and Inquiline Associates of *Anthophora linsleyi*

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Relatively few discussions have been published of parasites, predators or inquilines associated with North American bees of the genus *Anthophora*. Rau (1922 *et seq.*) and Frison (1922) have recorded some of the associates of *Anthophora abrupta* Say, Hicks (1926) those of *A. neomexicana* Cockerell, and Mickel (1928) those of *A. occidentalis* Cresson. The work of Mickel was notable in that he recorded the number of infested cells (out of 249 containing living insects) and made an attempt to evaluate the effects of the associated species on the population of the host. In the following pages data is given on twenty-two species of insects associated with *Anthophora linsleyi* Timberlake in three localities in California. The data were obtained by both field and laboratory observations and by an analysis of 2679 *Anthophora* cells. About two-thirds of the species were sufficiently abundant to enable the writers to definitely determine their relationship with their host.

Anthophora linsleyi Timberlake (1940) is a relatively common bee in areas adjacent to the Mojave Desert, California. It nests gregariously, sometimes in very large numbers, either in banks or flat ground. Apparently the species requires a hard-packed, dry, sandy conglomerate soil in an area where water is available throughout the nesting season. When banks are utilized, exposures which receive the early morning sun are usually selected for nesting sites.

The nest burrows of *linsleyi* are similar to those of other species of *Anthophora* but lack a projecting entrance tube or turret. In banks, the burrow enters at right angles to the surface, inclines downward sharply at a depth of about an inch, and continues as a simple or irregularly forked tube. In densely populated sites modifications are frequently required. The series usually comprises from three to six cells, which are of the normal jug-like shape characteristic of the genus, with the internal dimensions averaging about 10 x 7 mm. When the cell form has been completed, the inner surface is waxed and provisioned to about one-fourth of its depth with pollen. The surface of the pollen mass is covered with a mixture of nectar and water upon which the egg is deposited. After oviposition, the cell is capped with a circular mud plug which is waxed on the concave inner surface. The hatching larva rapidly consumes the stored food and by late summer has attained the prepupal stage (Fig. 3). The fall and winter are passed as an inactive prepupa and

¹ The writers wish to express their appreciation to Mr. G. E. Bohart who materially assisted them during the collection of field data, and to Miss Margaret C. Walker who took the habitat photographs for Figs. 1 and 2.

pupation occurs in the early spring. Under laboratory conditions, the average length of the pupal period of the male was 38 days, of the female 43 days, but in the field this period is sometimes shortened by as much as ten days. After transformation, the adult remains for a day or two in the cell and emerges when weather conditions are favorable. The species is proterandrous and the males normally precede the females by a week or ten days, usually emerging about the middle of March. They spend the days at flowers or flying about the nesting sites, assembling gregariously in resting burrows in the late afternoon. Early in the season the females also spend the night in resting burrows or in old tunnels, but when nest construction has begun, they utilize the new burrows for this purpose. In two localities, the females were observed to collect pollen only from *Salvia carduacea*.

This pollen is bright red and in these areas the bee larvae and pupae have a distinct orange or orange-red color. At a third locality, two or more undetermined flower species were utilized as pollen sources. The pollens were pale yellowish and orange and the bee larvae and pupae were transparent white, yellow or orange in color, depending upon the pollen on which they had fed.

Anthophora linsleyi has been found by the writers nesting in three localities in the vicinity of Mojave Desert, California, although only two of these sites

TABLE 1.—Associated Parasites, Predators and Scavengers in
Nests of *Anthophora linsleyi*.

Locality	Little Lake, 10 mi. S., Inyo Co., California.		Bakersfield, 20 mi. E., Kern Co., California.	
	Number of cells	Per cent of total	Number of cells	Per cent of total
Cells examined	1920	100.00	759	100.00
Living <i>Anthophora</i>	909	47.34	370	48.75
<i>Anthophora</i> killed by mold	203	10.58		
<i>Hornia boharti</i> (Meloidae)	458	23.85	111	14.62
<i>Trogoderma ajax</i> (Dermestidae)	118	6.14	40	5.27
<i>Melecta californica</i> (Anthophoridae)	75	3.91	44	5.79
<i>Nemognatha apicalis</i> (Meloidae)	6	.31	44	5.79
<i>Anthrax</i> sp. nr. <i>fur</i> (Bombyliidae)	76	3.96	33	4.34
<i>Photopsis auraria</i> (Mutillidae)	42	2.19	19	2.50
<i>Photopsis sercus</i> (Mutillidae)			1	.13
<i>Hylemyia cilicrura</i> (Anthomyiidae)	20	1.04		
<i>Ptinus californicus</i> (Ptinidae)			32	4.21
<i>Lytta occipitalis</i> (Meloidae)			11	1.45
<i>Lytta pupurascens</i> (Meloidae)			29	3.82
<i>Lytta chloris</i> (Meloidae)			7	.92
<i>Monodontomerus montivagus</i> (Callimomidae)	5	.26	4	.52
<i>Triepeolus mojaviensis</i> (Nomadidae)			3	.39
<i>Chrysis</i> (<i>Chrysis</i>) sp. (Chrysididae)			3	.39
<i>Chrysis</i> sp. (Chrysididae)			3	.39
<i>Plodia interpunctella</i> (Pyrilidae)			3	.39
<i>Tineola biselliella</i> (Tineidae)			2	.26
<i>Oryzaephilus surinamensis</i> (Cucujidae)	5	.26		
Gen. et sp. incert. (Ichneumonidae)	2	.10		
<i>Stegobium paniceum</i> (Anobiidae)	1	.05		

have been investigated in detail. One of these areas is in Grapevine Canyon, ten miles south of Little Lake, on the east side of the Sierra Nevada Mountains, near the Inyo-Kern County line. In this locality the bees were nesting in a low bank of hard, sandy conglomerate about sixty yards from a permanent stream. The bank was about four feet high and twenty-five or thirty feet long (Fig. 1).

A second locality was along Caliente Creek, about twenty miles southeast of Bakersfield, Kern County, near the entrance to the Tehachapi Pass. In this area the bees were nesting along a high, clay and sandstone bluff within 75 feet of a stream (Fig. 2). The population was distributed in a number of dense separate groups. Between the bluff and the stream, flowers were abundant, particularly *Lupinus* sp. and *Salvia carduacea* (March and April) and *Phacelia* sp. (May), but only the last two were utilized for pollen.

The third area (type locality) was near the junction of Deep Creek and the Mojave River, at the base of the San Bernardino Mountains. Here the bees were nesting in the middle of a moderately well-travelled dirt road. The location of the colony made a close examination impossible and observations in this area were confined to flight behavior, pollen visits and a study of the parasites flying about the nesting sites. The females, as in the Bakersfield area, collected pollen from *Salvia carduacea*, a fact which necessitated a flight of more than a mile from the nesting region.

HORNIA BOHARTI Linsley

Figs. 3, 4

Hornia boharti is the most important of the meloid parasites of *Anthophora linsleyi*. In the Bakersfield area 24 per cent and near Little Lake 15 per cent of the cells examined were found to be infested with this species. The adult beetles are wingless (Fig. 4) and ordinarily never come to the surface of the ground. The normal life is two years, the first winter and most of the following year being spent as a fifth instar larva (Fig. 3) within the intact exuviae of the fourth instar. In the winter of the second year, the larva transforms to the sixth instar within the fourth and fifth larval skins. Pupation follows and the second winter is passed as an adult within the exuvial capsule. In early February the male cuts a lateral hole in the side of his cell and tunnels along the edge of the series until he reaches a cell occupied by a female. Meanwhile, the female has cut a terminal opening in her cell sufficiently large for her head and antennae to protrude. The male enters through this hole and copulation takes place within the cell. The period of copulation ranges from a few minutes to half an hour, after which the male leaves and may or may not mate with another female. Occasionally the female will receive another male. After mating, the female almost immediately begins oviposition. This process continues for as long as eight weeks, during which time an average of 549 eggs is laid. Under laboratory conditions, the incubation period averaged forty-three days and eclosion of the larvae extended over an equal period. The primary larvae crawl past the dead or dying female and work their way to the surface of the ground. Here they are very active, even

in the hot sun, and if suddenly displaced by wind, are capable of spinning a fine silken thread which can support their weight. The larvae, when moving over the surface of the ground, continuously elevate their heads and spread their mandibles. When contact with a bee has been made they attach themselves to single hairs by means of their toothed mandibles. Upon male bees, the larvae are most commonly found on the ventral hairs of the thorax, on female bees, they are usually attached to those of the propodeum. Whether or not there is an exchange of larvae during copulation has not been established, although the position of the larvae at least suggests this possibility.

The primary larva gains access to the host cell through the medium of the female bee. When it is finally enclosed in the cell, it locates and destroys the bee egg. Immediately after the egg has been consumed, the larva migrates to the upper, dry portion of the cell and transforms to the second instar (all laboratory attempts to induce this development in the absence of an insect egg were unsuccessful). The third and fourth instars follow rapidly while the store of pollen and nectar is consumed. The orange-colored fifth and sixth instars are inactive and remain within a capsule of exuvial skin.

The most important competitor of *H. boharti* in the Bakersfield area was *Nemognatha apicalis*. However, although it was found that both species are commonly introduced into the same cell by the host bee, in every case investigated only the *Hornia* larva was successful in reaching maturity. No secondary parasites of *Hornia* were found in any of the areas under observation, although, in one case, larvae of *Hylemyia cilicrura* were observed to feed upon the eggs.

NEMOGNATHA APICALIS Le Conte

Fig. 5

Nemognatha apicalis is the second most important meloid parasite of *Anthophora linsleyi*. In the Bakersfield area 5.79% of the cells examined were infested with this species although near Little Lake, the percentage of parasitism was only 0.31%. From the time when the primary larva gains access to the bee cell, the early larval development is similar to that of *Hornia*. The winter is passed in the fifth larval instar. This overwintering larva is about the same size as that of *Hornia boharti*, but is reddish in color and is distinctly concave on the ventral surface (Fig. 5). Like *Hornia*, it is an inactive form which remains enclosed in the exuviae of the fourth instar. Transformation of the sixth instar occurs in the spring, within the exuviae of the fourth and fifth instars. This larva may then either transform directly into a pupa, or into a seventh instar. In the former case, the life cycle is usually completed in a single year, but in the latter, it is capable of an indefinite extension of time (one or more years). The seventh instar larva is protected by a tough, dark, resistant capsule formed by the exuviae of the fourth, fifth and sixth instars, the latter two exuviae being very closely adherent. In either case, the adults emerge in late March and early April and fly to flowers, particularly those of the Compositae. Their food appears to consist solely of nectar, and in the laboratory they may be kept alive for weeks by feeding them with a solution of honey and water. Under field conditions the eggs are

laid on flowers but the method by which the primary larvae gain access to the bee cells has not yet been established. In the area where the infestation was greatest, the *Anthophora* and *Nemognatha* were visiting different flowers. It is possible, as Pierce (1904) has suggested for rhipiphorid beetles, that the young larvae gain access to the proper bee flowers by transportation on more catholic, polytropic hosts.

LYTTA OCCIPITALIS Horn

Fig. 6

Lytta occipitalis is one of the characteristic meloid species of the southern San Joaquin Valley. As a parasite of *Anthophora linsleyi*, it has been found only in the Bakersfield area, where 1.45% of the cells examined were infested. The primary larvae, having gained access to the host cell, develop very rapidly but may require the contents of more than one bee cell in order to complete their growth. As fully fed fourth instar larvae they leave the anthophorid series and construct an overwintering cell an inch or more behind the bee burrow. This cell is larger than that of the host bee, averaging 10 x 22 mm. in internal dimensions. The winter is passed as a naked, fifth instar larva (Fig. 6) with the exuviae of the fourth instar attached to the apex of the abdomen. This larva is entirely inactive and lies motionless on its dorsum. In the late spring (April) it transforms into a more active but non-feeding sixth instar (Fig. 6). It remains in this stage for from two to three weeks during which time it tunnels toward the surface and constructs a pupal cell. Pupation follows and normally requires about eight days. The adults emerge in early May and feed on the petals of flowers and to some extent upon pollen. They are gregarious, gathering on plants, where mating takes place. Presumably the eggs are deposited in or on the ground and the primary larvae crawl up the plants to contact the host, but this fact was not definitely established. In the laboratory a few egg masses were obtained in glass vials.

LYTTA PURPURASCENS Fall

Fig. 7

Lytta purpurascens occur in the southern San Joaquin Valley and has been recorded from as far south as San Diego County. Near Bakersfield 3.82% of the cells of *linsleyi* were infested with this species.

Its biology is similar to that of *L. occipitalis*, but the adults emerge a month or more earlier, usually in March. They gather gregariously on flowers of *Lupinus* and *Salvia*.

LYTTA CHLORIS Fall

Lytta chloris is smaller than *L. purpurascens* and the adults are brilliant green with cinerous pubescence. Its life history is very similar to that of the two previous species, but due to its smaller size, the larva requires the contents of but a single bee cell. As a parasite of *Anthophora linsleyi*, this species was found only in the Bakersfield area, where but 0.92% of the cells examined were infested.

TROGODERMA AJAX Casey²

Fig. 8

Trogoderma ajax is primarily a scavenger in old used cells of *Anthophora*. The larvae feed on old exuviae, insect parts, dead insects and occasionally unused pollen. The writers have never observed them attacking living insects or found any evidence to suggest that this ever takes place. However, they are not infrequently responsible for the death of bees by prematurely cutting into cells and exposing the occupants to the external environment or to mold and other parasites or predators. The length of the life cycle varies as does the number of larval instars. Pupation occurs in the last larval skin (Fig. 8) and the adults emerge and are active during March, April, May and June.

PTINUS CALIFORNICUS Pic

Fig. 9

Ptinus californicus has been reared by the authors from the cells of two other species of *Anthophora* in both of which it is uncommon. Normally, it is a depredator in the nests of Osmiine bees. It was found at Bakersfield in only 4.21% of the *Anthophora* cells examined and was taken only in those areas where the host population was most dense. In the nests of *Osmia*, the species passes the winter in the adult stage within cocoons. Emergence is accomplished in early spring by means of two steps; the first involves cutting a terminal hole in the cocoon, the second, making a single lateral hole in the cap of the bee cell. The beetles are not synchronous with their host and adults may be taken several weeks prior to the emergence of the bees. They are active in late afternoon when they emerge in large numbers from cracks, crevices and bee burrows and wander about on the face of the cliffs. Mating takes place on the surface of the ground. After mating the female deposits her eggs directly in the open cells being provisioned by the bees even though the bee is usually present in the burrow at the time. The eggs hatch after an incubation period of 18 to 20 days and the young larval bee dies, probably either as a result of starvation or the liberation of toxic substances in the food mass. The period of larval development varies with the amount of available food and climatic factors, although under optimum conditions, it is completed in about eight weeks. There are five larval instars and during the fourth instar, the larva constructs a cocoon among its thread-like feces (Fig. 9), attaching the cocoon to the side of the bee cell. The cementing material is secreted from the anal opening and when dry, is brittle and semi-transparent. The average number of beetles in a single *Osmia* cell is four, but variation from one to six has been observed. In the nests of *Anthophora linsleyi*, *Ptinus* is not usually a depredator, but lives mainly in old cells, particularly those which had been previously occupied by *Hornia*. Under these conditions, the larvae feed upon fecal pellets and old pollen and only one larval occupant occurs in a cell. No parasites of *Ptinus californicus* were taken in the Bakersfield area but a small chalcidoid wasp has been reared from their cocoons in the nests of *Osmia lignaria* Say at Pittsburg, California.

² Identification by H. S. Barber.

ORYZAEPHILUS SURINAMENSIS (Linn.)

Near Little Lake larvae or adults of this common storage pest were found in five cells of *Anthophora linsleyi*. They appeared to be feeding upon old pollen.

STEGOBIUM PANICEUM (Linn.)

This species, like the preceding, probably feeds on the pollen store of the bee. Near Little Lake, adults and larval remains were found in a single cell of *A. linsleyi*.

ANTHOCOPA XEROPHILA (Cockerell)³

Anthocopa xerophila is one of a number of species of Osmiine bees which are associated with anthophorids through the appropriation of their used burrows. The *Anthocopa* cells are constructed with macerated plant material, and provisioned with moist pollen upon which the egg is laid. The young larvae complete their growth in a few weeks and spin a tough yellowish cocoon. Pupation and transformation to the adult occur in the spring. Near Little Lake, hundreds of *xerophila* were flying about the nesting site of *A. linsleyi*, and in some areas of the bank, a large proportion of the old but intact burrows had been appropriated. Our observations suggest that the *Anthocopa* have little effect upon the population of *Anthophora* except through the possibility of introduction or overflow of new parasites or predators. The presence of *Ptinus californicus* in the nests of *A. linsleyi* near Bakersfield may well have been the results of such a relationship since the *Ptinus* is normally associated with Osmiine bees.

MELECTA CALIFORNICA Cresson

Fig. 10

This parasitic anthophorid is widely distributed along the Pacific Coast of North America. It is commonly associated with *Anthophora urbana* Cresson (Linsley, 1939) but has been reared by the writers from the nests of *A. edwardsii* Cresson and *A. stanfordiana* Cockerell as well as from those of *A. linsleyi*. The female deposits her egg just inside the opening of the uncompleted cell of the host. The *Melecta* egg is similar to that of *Anthophora linsleyi* but smaller and is attached to the wall of the cell by one end. The incubation period of the egg is shorter than that of the host and the hatching larva destroys the egg of the latter by means of its long, slender mandibles. The *Melecta* larva then consumes the pollen store and when mature, constructs a large cocoon (Fig. 10), which completely fills the cell. This cocoon is tough, brown and uniform in texture, quite unlike that of other associated parasites. The winter is passed as a prepupal larva within the cocoon and pupation occurs in the spring. The pupa, in contrast to that of its host, has a pair of spiny tubercles on the mesonotum, and is capable of considerable activity. Under laboratory conditions the pupal period averages 30.5 days. The adults emerge in April and May and the peak of their activity is from four to six weeks after the emergence of their host. They are numerous about the nesting site and commonly visit flowers in search of nectar. The larvae are

³ Identified by C. D. Michener.

subject to secondary parasitism by most of the parasites of *Anthophora linsleyi*, particularly *Photopsis* and *Anthrax*.

TRIEPEOLUS MOJAVENSIS Linsley

Little is known of the biology of this species other than that it is a parasite of *Anthophora linsleyi*. It was found both at Deep Creek and near Bakersfield. The percentage of parasitism in the latter locality was only 0.39%. In the former area three examples, all females, were taken flying about the nesting site and exploring burrows.

PHOTOPSIS AURARIA (Blake)*

This species is the commonest mutillid parasite found associated with *Anthophora linsleyi*. The adults are nocturnal and are active toward the close of, or immediately following, the anthophorid season. The female burrows into the bank along the side of a completed *Anthophora* series and cuts a conical pit at the basal (pollen) end of a cell. Through this opening the ovipositor is inserted and the egg is laid. The young *Photopsis* larva usually attacks the prepupal bee. Upon the completion of feeding and growth, it spins a loose network of threads within the cell wall. Within this framework a tough, brown, diagonally-placed cocoon is constructed. The winter is passed in this cocoon and pupation occurs late in the following spring or early summer (average length of pupal period: nineteen days). The percentage of parasitism near Little Lake was 2.19% of the cells examined, near Bakersfield, 2.50%. In both areas the species was also reared from *Melecta californica*, but whether or not it attacks non-hymenopterous parasites of *linsleyi* is unknown. The *Photopsis* itself is frequently subjected to parasitism by *Monodontomerus montivagus* and as many as 21 specimens have been reared from a single cocoon.

PHOTOPSIS SERCUS Viereck*

One male reared from a cell of *A. linsleyi* near Bakersfield, Calif.

CHRYSID (CHRYSID) sp.

In the locality near Bakersfield, three cells of *A. linsleyi* were found which contained fragments of *Chrysis* (*Chrysis*) sp. It was not possible to identify the species with certainty and there were no active adults in the area at the time (late March and early April).

CHRYSID sp.

This species was also represented by fragments in three cells of *linsleyi* from near Bakersfield. It is probable that neither this nor the previous form is an important parasite of the *Anthophora*.

MONODONTOMERUS MONTIVAGUS Ashmead

Monodontomerus montivagus is a common parasite of bees, particularly of the gregarious anthophorids. In the Bakersfield area 0.52 % of the cells of *A. linsleyi* were parasitized; at Little Lake 0.26%. The females hibernate in

* Identified by C. E. Mickel.

the nesting area and oviposit in early spring. In the field the number of individuals in a cell averaged 26 for females and 40 for males. Cells containing females outnumbered those with males in a ratio of three to one, and only one cell with mixed sexes was encountered (23 ♀♀, 7 ♂♂). The pupal period requires from 18 to 20 days. Emergence of both sexes occurs in late spring, with the males preceding the females by a few days. Mating takes place immediately upon the appearance of the females and the latter mate only once although a male may fertilize several females. Copulation is preceded by a preliminary "courtship" pattern. The male assumes a position far forward on the back of the female, with his mouthparts in the space between her head and thorax. The front legs grasp the neck and the hind legs are free in the air. The antennae are then placed between those of the female, laid flat on the front of her head and then vibrated rapidly on her face. After several minutes of this activity, the female extends the tip of her abdomen, the male dismounts, and copulation takes place for a few seconds. The males do not seem to be able to distinguish between mated and virgin females and spend much time in unsuccessful "courtship" of those which have already mated. Although the males usually die within a few days after mating, the females are long-lived and spend the day on the surface of the cliffs, flying about and crawling into burrows. Oviposition apparently does not occur until early in the following spring. The first instar larvae have been recovered from the intersegmental membranes of prepupal bees. Normally only the prepupal stage is attacked but in one case, the writers reared *Monodontomerus* from an unemerged adult *Anthophora*. As a parasite of *A. linsleyi*, this species is relatively unimportant. However, as a secondary parasite of *Photopsis* it was found in 37 per cent of the cells examined. Only about half as many *Monodontomerus* emerge from a single *Photopsis* cocoon as from a normal cell of *Anthophora*. Since the *Photopsis* are active after the bee season and tunnel into the banks in order to oviposit, the *Monodontomerus*, which lay their eggs even later, have ready-made access to the same cells. This probably explains the high percentage of parasitism in *Photopsis*.

ICHNEUMONIDAE (Gen. et sp. incert.)

In two cells of *Anthophora linsleyi* from near Little Lake, dead pupae of an undeterminable ichneumonid were found. Its status as a parasite of the bee is unknown.

HYLEMYIA CILICRURA Rondani⁴

Hylemyia cilicrura was found associated with *Anthophora linsleyi* near Little Lake where 2.7 per cent of the cells were affected. The flies were taken as full-grown larvae, pupae and freshly-emerged adults in the first week of April, and adults continued to emerge in the laboratory for a period of three weeks. The pupae were commonly found in the surrounding earth or burrows at a distance of from one-half an inch to an inch away from the host cell. The number of individuals varied from one to five with an average of four

⁴ Identified by C. H. Curran.

to each cell. Frison has recorded a related Anthomyid, *Pegomyia affinis* Stein, from the cells of *Anthophora abrupta* Say, and interpreted the association as being that of a scavenger on old pollen and other detritus in the cells. *Hylemyia cilicrura* is known in economic literature as the seed corn maggot (for an account of its life history, immature stages, etc., see Hawley, 1922). It attacks a variety of young plants and is also said to breed in decaying vegetation and in manure. This or a related species was recorded by Riley (1878) as feeding upon locust eggs in Kansas and other western states. Near Little Lake two larvae, taken by the authors, were feeding on a freshly-laid egg mass of *Hornia boharti* and several others on prepupal and pupal bees. However, in the latter cases it was not possible to determine whether or not the flies had been responsible for the death of the bees. Thus, the exact status of this species as a parasite or scavenger has not been established, but its effects, if any, are probably slight.

ANTHRAX sp. near FUR O. S.⁵

Fig. 12

This species was the only observed Bombyliid attacking *A. linsleyi*. The adults have the same period of activity as the bees and spend most of their time about the nesting area. Mating takes place during the warmest part of the day. The pairs remain in copulation for a considerable period of time and when disturbed they will fly away without separating. After each mating, the female hovers about the nest entrances and throws two or more eggs into each burrow. No discrimination between old and new burrows was evident. The incubation period of the eggs and the activities of the primary larvae were not determined. However, the latter apparently do not attack the bee immediately, but wait until it has attained the prepupal stage. The larvae are usually found attached to the intersegmental membrane behind the head. When ready to feed, they pierce this membrane and consume the body contents of the bee. On one occasion an immature bombyliid larva was found attacking a bee pupa, further evidence that they wait a considerable length of time before attacking the host. Full-grown larvae may occasionally be found in March although most individuals have pupated by that time. The adults emerge at about the same period as the female bees. The pupal bombyliid cuts its way to the surface of the bank by rotary motions and use of the head spines. At the surface emergence takes place and the adult fly is capable of flight almost immediately. No observations were made upon the food habits of the adults, but they were never seen to visit flowers or suck nectar.

MYOPA RUBIDA Bigot

This species of conopid is a parasite of adult *Anthophora* in the Bakersfield area. Three individuals were taken as live puparia within the abdomen of the bees. However, the percentage of parasitism is probably too low to have much effect on the total population.

⁵ Identified by R. H. Painter.

TINEOLA BISELLIELLA Hummel⁶

This species was found in two cells of *Anthophora* near Bakersfield. It is apparently a scavenger on old insect parts and detritus.

Plodia interpunctella (Hubner)

Plodia interpunctella appears to be a scavenger on old pollen. It was reared from one *Anthophora* cell in the Bakersfield area.

Host Relationships

The various species of insects associated with *Anthophora linsleyi* in the localities investigated may be roughly divided into several groups with regard to their host relationships as follows:

GROUP I. Scavengers living on excess pollen, insect parts, etc., in old cells; not injurious to the bee.

- | | |
|--------------------------------------|----------------------------------|
| (1) <i>Stegobium paniceum</i> | (4) <i>Tineola biselliella</i> |
| (2) <i>Oryzaephilus surinamensis</i> | (5) <i>Plodia interpunctella</i> |
| (3) <i>Plinus californicus</i> | |

GROUP II. Scavengers which do not attack living insects but which indirectly cause the death of the host by opening its cell and exposing it to the external environment.

- (1) *Trogoderma ajax*

GROUP III. Depredators which live at the expense of the food store of the host and usually cause its death.

- (1) *Plinus californicus*

GROUP IV. Facultative predators which may either feed on the eggs of the host or may be a scavenger upon vegetable materials.

- (1) *Hylemyia cilicrura*

GROUP V. Species which are egg predators in the first instar, pollen feeders in subsequent instars.

- | | |
|--------------------------------|-------------------------------------|
| (1) <i>Hornia boharti</i> | (5) <i>Lytta chloris</i> |
| (2) <i>Nemognatha apicalis</i> | (6) <i>Melecta californica</i> |
| (3) <i>Lytta occipitalis</i> | (7) <i>Triepeolus mojavenis</i> (?) |
| (4) <i>Lytta purpurascens</i> | |

GROUP VI. External parasites or predators of larvae or pupae.

- | | |
|---|--------------------------------------|
| (1) <i>Anthrax</i> sp. near <i>fur</i> | (4) <i>Monodontomerus montivagus</i> |
| (2) <i>Chrysis</i> (<i>Chrysis</i>) sp. | (5) <i>Photopsis auraria</i> |
| (3) <i>Chrysis</i> sp. | (6) <i>Photopsis sercus</i> |

GROUP VII. Internal parasites of larva.

- (1) Undet. Ichneumonid.

GROUP VIII. Internal parasites of adult.

- (1) *Myopa rubida*

⁶ Identified by H. H. Keifer.

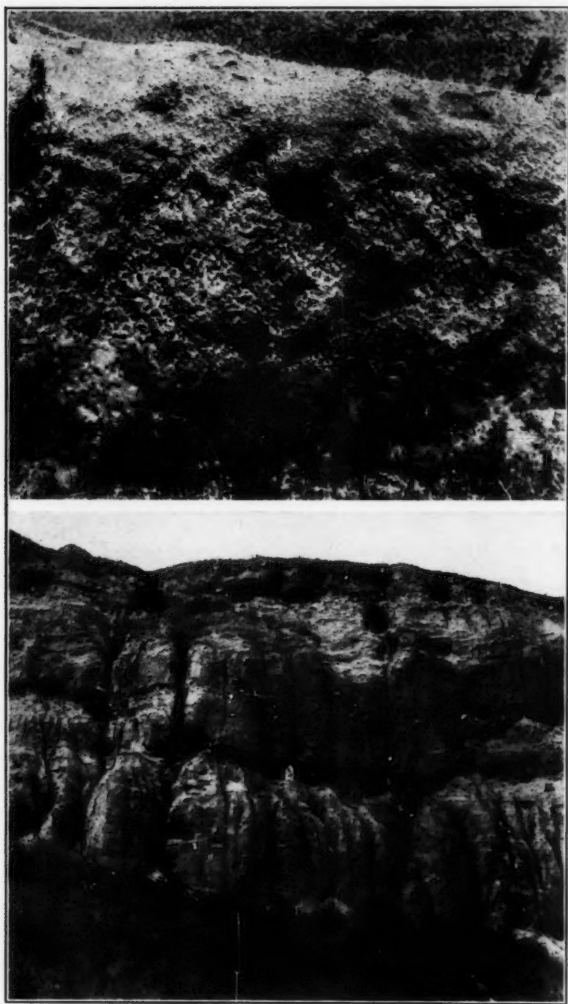


Fig. 1. Nesting site of *Anthophora linsleyi* Timb. near Little Lake, Inyo County, Calif.

Fig. 2. Nesting area of *Anthophora linsleyi* Timb. near Bakersfield, Kern County, Calif.

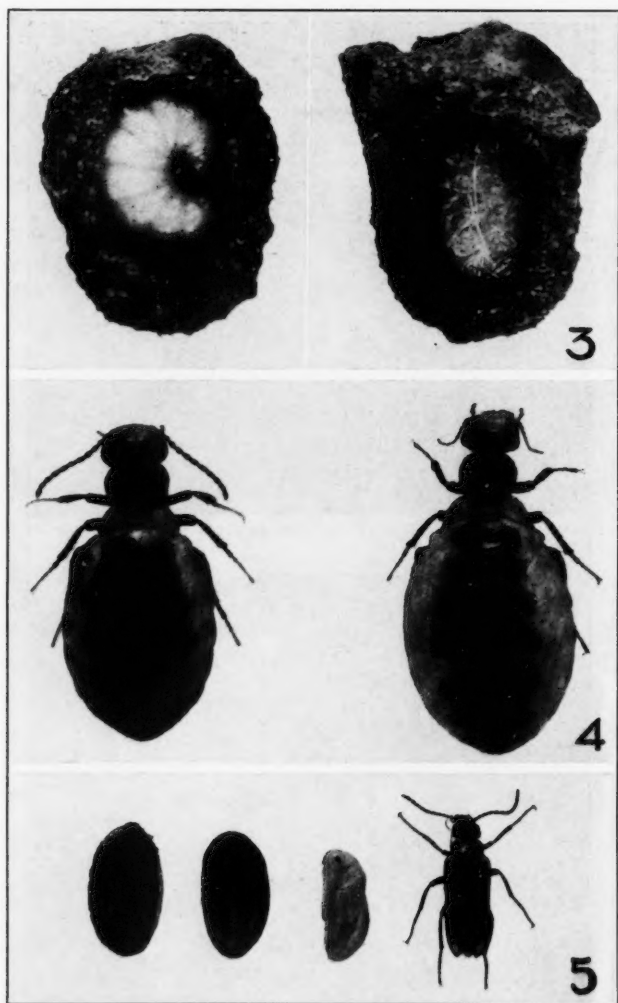


Fig. 3. Cells containing prepupal larva of *Anthophora linsleyi* Timb. (left) and fifth instar larva of *Hornia boharti* Linsley (right), $\times 3$.

Fig. 4. *Hornia boharti* Linsley. Adult male, left, adult female, right, $\times 5$.

Fig. 5. *Nemognatha apicalis* Lec. Fifth instar larvae within exuvial capsule (left) and removed from exuvial capsule (left center), pupa and adult, $\times 2$.

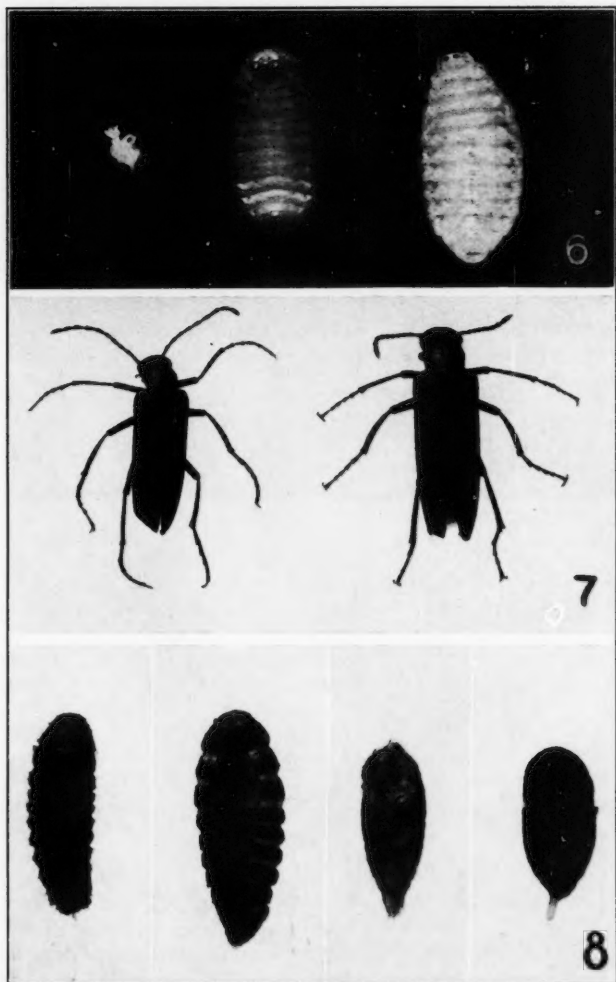


Fig. 6. *Lytta occipitalis* Horn. Eggs, (left) fifth larval instar (center), sixth larval instar (right).

Fig. 7. *Lytta purpurascens* Fall. Adult male (left) and female (right).

Fig. 8. *Trogodermia ajax* Casey. Larva (left), pupa within last larval skin, pupa removed from skin, adult (right).

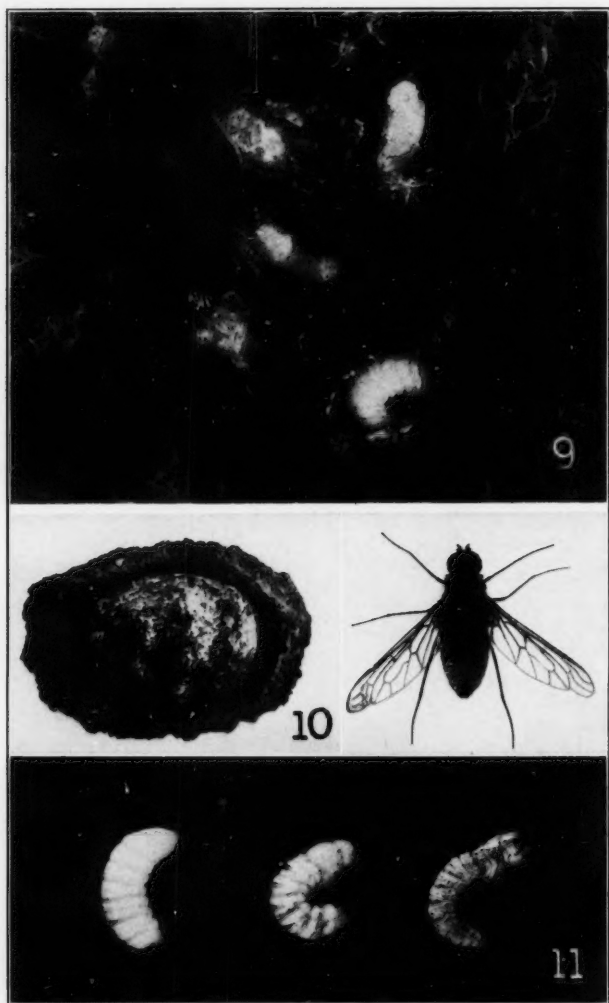


Fig. 9. *Ptinus californicus* Pic. Larvae and pupae in mass of fecal strands.

Fig. 10. *Melecta californica* Cresson. Cocoon within cell of *Anthophora*.

Fig. 11. *Anthrax* sp. nr. *fur* O. S. Adult (above), larva (lower left), pupa (lower center), pupal skin (lower right).

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A New *Cuterebra* (Diptera; Cuterebridae) from Iowa With Notes on Certain Facial Structures

Herbert T. Dalmat

Cuterebra angustifrons n. sp.

Holotype (Male). In collection of author. One specimen reared from a larva taken from *Peromyscus leucopus noveboracensis*, October, 1940, at Ames, Iowa. Adult emerged August 21, 1941.

Length, 13.1 mm. Mesonotum at widest point, 4.5 mm.; scutellum 3.6 mm. wide and 1.8 mm. long. Maximum width of abdomen, 5.8 mm.

Width of cephalic capsule through vertex, 6.2 mm. Distance between eyes at vertex, 1.1 mm. (Ratio 5.5 to 1.) Ocellar triangle small, almost equilateral, length of base, 0.51 mm., length of arms, 0.48 mm., strongly raised above front. Mesovertex (see plate) 0.30 mm. long. Prevertex (see plate) long, narrow, extending anteriorly from sides of apical ocellus, without posterior arms; distance from apex of ocellar triangle to end of prevertex, 0.44 mm. Prevertex with well-defined pit about .30 mm. from apical ocellus.

Antennal grooves together forming a circular depression, completely circumscribed. Carina concave when viewed in profile. Antennal depression pollinose except for strongly shining, almost black ventro-lateral regions. Antennae and aristae brown. Antennae covered in part by silvery pollinosity; a cluster of white hairs on first antennal segment, only a single white hair on shiny area on outer margin of second segment. Aristae ciliate above, with two hairs below on distal end.

Cheek grooves indistinct and shallow. Entire head below cheek grooves white pollinose and covered with white hair except for two shining areas on each side, a brown one on lower margin of eye and a larger black one midway between it and the mouth. White pollinosity of buccae extending slightly up the parafacials. Frontal vitta covered with grayish-white pollen. Parafacials, parafrontals, and prevertex dark brown, shining. Black hairs sparsely covering frontal vitta and most of parafrontals. A few white hairs similarly covering parafacials and ventro-lateral regions of parafrontals near eyes. Ocellar triangle and mesovertex clothed with black hairs more bristly than on rest of head.

Three white pollinose areas contiguous with inner margin of each compound eye. Lowest area just above cheek groove, contiguous with, and parallel to, inner margin of eye, and continuous with pollen of bucca. Second area triangular, immediately dorsal to ridge running laterad from ptilinal suture almost to eye. Uppermost spot contiguous with, and extending parallel to,

margin of eye just above dorsal limit of antennal depression. Occiput completely white pollinose, clothed with white hairs.

Thorax black above with faint grayish bloom, slightly shining; black hairs on dorsal surface .44-.73 mm. long, the distance between adjacent hairs averaging .08 mm. Pleurae covered by white pollinosity and very dense white hairs, little longer than those on dorsum, the distance between adjacent hairs about 0.3 mm. No cluster of black hairs near anterior dorsal corner of mesopleuron; two dark brown shining areas above insertion of anterior coxa. Legs clothed with black pubescence except for bands of white hair running down outside of femora of forelegs; legs lacking pollinosity.

Abdomen iridescent blue. First segments sparsely covered by whitish pollen, a single row of short white hairs on anterior margin. Dorsal and lateral regions of second, third, and fourth abdominal segments without pollen except at the extreme lateral borders where there are nonsymmetrical, pollinose areas interrupted by small, dark brown, shining spots. These pollinose areas invested with white hair longer than other hair on these segments. Hair on dorsa of second through fourth segments black; that on second segment increasing in length laterally as in *C. buccata* (Fabricius) and *C. peromysci* Dalmat, about twice as long and more flexuous than hair on third and fourth segments. Hairs on third and fourth segments .30-.35 mm. long, about .08 mm. between adjacent ones, more bristle-like than those on thorax.

Fifth segment completely encircled by dense white pollen and white hairs except for a few dark, shining spots. Strongly shining black band at posterior about .03 mm. No cluster of black hairs near anterior dorsal corner of mesomargin of segment. White hairs of this segment 0.2-0.4 mm. long, about .08 mm. between them.

Sixth segment with white pubescence similar to that on fifth. Pollen in wide band on posterior border, none elsewhere. Sixth segment hidden beneath fifth, surrounding genitalia.

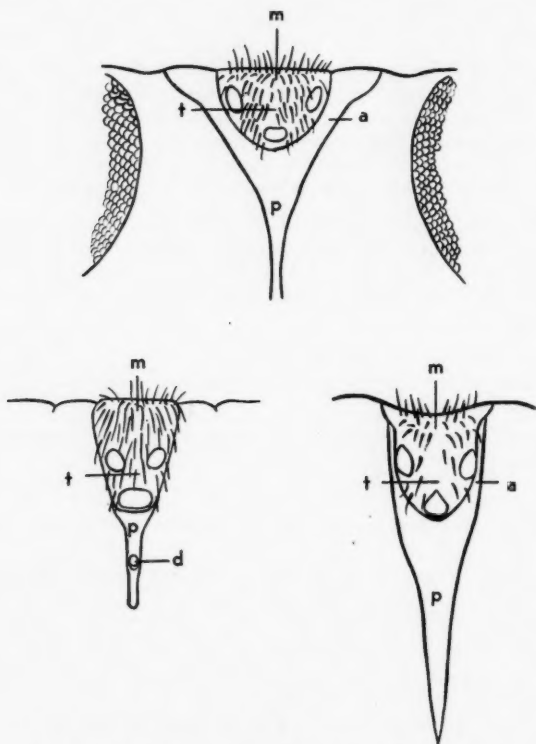
Genital claspers clothed with white hair. Sternites gray pollinose, with long black hair.

Cuterebra angustifrons is most closely related to *C. peromysci* Dalmat and to *C. fasciata* Swenk.

The mesovertex of *angustifrons* is longer, and the ocellar triangle smaller, than on *peromysci*. The prevertex of *peromysci* is elongate and triangular, 0.80 mm. long, and raised above the level of the front; the posterior arms of the prevertex border the ocellar triangle for the entire length of its sides. The prevertex of *angustifrons* does not have posterior arms bordering the ocellar triangle and it is about level with the plane of the front. The facial depression of *angustifrons* is circular rather than oval, the cheek grooves shallow. The white hairs on the pleura are little longer than the hairs on the dorsum of the thorax, while in *peromysci* the difference in the length of the hairs on the two areas is much more marked. *C. angustifrons* also differs from *peromysci*

by having the scutellum much wider in relation to the rest of the mesonotum, by lacking a pollinose spot near the dorsal limit of the facial depression, by not having pollen on the dorsal sclerites of the first four abdominal segments, by the absence of a cluster of black hairs near the anterior dorsal corner of the mesopleuron, and by lacking a cluster of white hairs on the second antennal segment.

C. angustifrons differs from *fasciata* as follows: Its facial depression is completely circumscribed rather than produced ventrally; it lacks a cluster of white hairs on the second antennal segment; it has a shiny area at the base of the eye and another between it and the mouth; there is pollen on several of the abdominal segments rather than on the fifth only; and the pleural hairs are longer.



Vertical areas of *Cuterebra buccata* (Fabricius) (top), *Cuterebra angustifrons* n. sp. (lower left), and *Cuterebra peromysci* Dalmat (lower right); m, mesovertex; t, ocellar triangle; p, prevertex; a, posterior arms of prevertex; d, pit.

The author has found that the vertical area of the front of various species may be useful in specific classification. Definitions of the terms used in the above description for these parts and figures illustrating them in three species are given below.

Ocellar triangle. The triangular area formed by the ocelli. Clothed with bristle-like hairs, much heavier than those on rest of head.

Mesovertex. The area of the front between the occiput and the ocellar triangle, bordered laterally by the projections of the sides of the ocellar triangle to the occiput. Invested with bristle-like hairs, similar to those on ocellar triangle, in several species examined.

Prevertex. The elongate, shining area anterior to the ocellar triangle, often triangular, extending anteriorly on the front, sometimes pollinose, never clothed with erect hairs. The prevertex may have posterior arms bordering the sides of the ocellar triangle, which may taper out along the triangle or be prolonged to the occiput.

A New Astomatous Ciliate from the Newt, *Eurycea bislineata* (Green)

Maire Weir Kay*

In the course of examination of the intestinal contents of 21 specimens of *Eurycea bislineata* (Green) collected at Oxford, Mass., during the summer of 1939 a single newt was found of which the small intestine was heavily infested with an astomatous ciliate. Observations and measurements were made on the living organisms which were later killed with hot saturated aqueous mercuric chloride solution containing 2% of acetic acid. These specimens were ultimately stained, some with acid carmine, others with Ehrlich's acid haematoxylin with or without a counterstain of eosin.

Cursory examination showed that the ciliates were members of the family Haptophryidae Cépède and related to the genera *Sieboldiellina* Collin and *Haptophrya* Stein in which uncini are lacking. To determine their exact relation to these genera has been more difficult due both to a noteworthy overlapping of characters in the specimens and to the varying reports that have been made concerning the morphology and relationships of this whole family.

An adequate taxonomical study of the Astomata was first made by Cépède (1910). In this study he creates the family Discophryidae, later Haptophryidae (Cépède 1923) to include four genera of ciliates characterized by

Présence presque constante d'une dépression en ventouse fixatrice à l'extrémité antérieure du corps (*Lachmannella* seule fait exception).

Système contractile constitué par un long vaisseau latéral.

Macronucleus en ellipse.

In differentiating the genera he uses the following characters:

<i>Un uncinus fixateur</i>	<i>Lachmannella</i> Cépède
<i>Deux uncini fixateurs. Acetabulum sans cils</i>	<i>Steinella</i> Cépède
<i>Pas d'uncinus fixateur</i>	<div style="display: inline-block; vertical-align: middle;"> <div style="display: inline-block; vertical-align: middle; font-size: 2em; line-height: 1;">{</div> <div style="display: inline-block; vertical-align: middle;"> Constriction en forme de cou. Ventouse bordée d'une rangée de cils...<i>Discophrya</i> Stein [<i>Sieboldiellina</i> Collin] Ventouse en fer à cheval montrant de très forts cils sur un rang ou sur deux rangs<i>Haptophrya</i> Stein </div> </div>

While indicating that there is probably a close phylogenetic relationship between the first three of these genera Cépède did not at this time undertake any division into subfamilies. Later (1923) he introduced three subfamilies; *Lachmannellinae* containing *Lachmannella*, *Steinellinae* which included *Steinella* and *Sieboldiellina* and *Haptophryinae* which contained solely the genus *Hapto-*

* I feel it essential at this point to express my appreciation of valuable assistance rendered to me in the preparation of this study by the late Professor John E. Guberlet of this department.

phrya. Bishop (1926) points out that the inclusion of *Sieboldiellina* in a subfamily of which one of the diagnostic characters is the possession of two hooklets for fixation is unjustified. Basing her decision on structure and mode of division this author has created an additional subfamily to contain *Sieboldiellina*. Consequently the current classification of the family as adopted by Bishop is:

Family Haptophryidae (Cépède, 1923)—Discophryidae (Cépède, 1910).

I. Subfamily Haptophryinae, two species, *H. tritonis* Certes, *H. gigantea* Maupas. [To this must be added *H. michiganensis* Woodhead 1928.]

II. Subfamily Lachmannellinae, *Lachmannella recurva* Cl. et Lach.

III. Subfamily Steinellinae, *Steinella uncinata* Schultze.

IV. Subfamily Sieboldiellinae, *Sieboldiellina planariarum* Siebold.

In view of the mixed characters of the organism under consideration in the present study it seems doubtful whether this extreme segregation of the genera is justifiable. If one followed the precedent of Bishop it would be necessary in this case to erect a new subfamily of doubtful significance for an organism having characters in common with both the first and fourth subfamilies under her system. Because of the unsatisfactory nature of such a proceeding and because the small number of genera and species known in the family render minute classification largely a matter of speculation it seems advisable, at least for the present, to revert to Cépède's earlier classification and consider the family as one in which the known similarities overlap too continuously to permit division into subfamilies.

In his description of *Sieboldiellina planariarum* Cépède mentions the following points; rapid movement, relatively small size (700μ), alveolar ectoplasm, relatively short cilia. To these Bishop adds 2 micronuclei apposed to the "megannucleus" and a peculiar thickened pad at the base of the sucker. This ciliate is known as a parasite of a number of species of Turbellarians. *Haptophrya*, on the other hand, is known only as a parasite of the intestine of amphibians (Maupas, Certes, Cépède, Woodhead); it may be very large, up to 1600μ ; rigid, non-contractile ectoplasm; cilia about 5μ , in rows, very numerous; movement slow; catenulation. Cohn (1904) identifies the micronucleus only during fission while according to Cépède it is constantly present and similar to that of *Anoplophrya*.

As will be brought out in the course of this study the species here under consideration cannot conveniently be fitted into either of these genera. It not only possesses some characters of each but others which are peculiar to itself.

MORPHOLOGY OF THE CILIATE

Figs. 1, 2, 3.

The protozoan taken from the intestine of *Eurycea bislineata* is of moderate size, the largest specimen not exceeding 700μ while the average individual, not a member of a catenula, reaches a length of 620μ . In form the body is roughly cylindrical and shows distinct dorso-ventral compression. Covering

the whole surface are very numerous short cilia which are slightly longer over the anterior dorsal portion of the body. The whole organism is definitely divided into head, neck and body regions by a constriction in the second seventh from the anterior end.

The anterior seventh or head region is significant as the seat of the attachment organ or sucker. Anterior to the sucker is a slight, proboscis-like prolongation of the dorsal part of the head. The sucker lies on the ventral surface surrounded by a thickened rim which is noticeably heavier on the posterior edge. Cilia line the whole concave surface of the sucker; these are particularly long and dense in the posterior part. There is, however, no determinable row of long cilia edging the sucker. The double pellicle which covers the entire animal is reflected over the surface of the sucker; here, as on the rest of the body, the bases of the cilia appear to lie within the pellicle. Beneath this is a very dense disk of granular cytoplasm, comparable to that described by Bishop for *Sieboldiellina*, from which myonemes extend out dorsally to the body wall and posteriorly through the endoplasm.

The elongated body is made up of strongly differentiated ectoplasm and endoplasm which are sharply marked off from one another in both living and fixed specimens. A rather simple, granular, rigid structure is characteristic of the ectoplasm. The endoplasm, on the other hand, is highly differentiated consisting of an amorphous fluid portion and a more solid fibrillar portion which is largely concentrated about the macronucleus and the posterior portion of the body. The movements of the living animal suggest that these fibrils have a contractile function more or less comparable to that of the myonemes of the sucker with which this fibrillar endoplasm is usually in contact.

The macronucleus is relatively large, as much as a fourth or fifth of the body length in some specimens, i.e., up to 125μ in length. It has the form of an elongated oval or ellipse and appears to be purely alveolar in structure. None of the chromatin spherules described by Maupas (1879) and later authors in *Haptophyra* can be identified; all the visible chromatin is located in the walls of the many alveolae that make up the nucleus. No micronucleus has been observed; nor do those specimens which are counterstained with eosin show anything equivalent to the eosinophile "micronucleus" of Woodhead (1928).

A contractile canal lies in the ectoplasm of the dorsal surface of the animal. It arises at a point just posterior to the small proboscis and extends posteriorly almost to the tip of the body. In normal individuals no pores are to be seen in the contractile canal; in the case of degenerating specimens in which the canal has become distended with fluid from 5 to 7 linearly arranged, oval openings to the dorsal surface may be visible. It seems probable from this that the pore in the normal animal is too minute to be seen in unsectioned material. The fully expanded canal may be up to 28μ in width, in this respect considerably exceeding *Haptophyra gigantea* ($18-21\mu$). The period of pulsation of the canal is about 45 seconds while Maupas reports a little over a minute for that of *H. gigantea*.

PHYSIOLOGICAL OBSERVATIONS

The movement of the animal is relatively rapid. While its linear progress is brought about by the dense coating of cilia there is, in addition, a writhing, wormlike movement which apparently originates in contractions of the fibrillar endoplasm.

The sucker is a thoroughly efficient attachment mechanism. Even in detached, free-swimming individuals it is found to be at least partially contracted and frequently contains debris from the intestinal wall and content. In the case of firmly attached specimens even the application of fixing fluid is not sufficient to cause them to relax their hold. Depression of the sucker is accompanied by and presumably brought about by contraction of the opposing groups of dorsally and posteriorly directed myonemes.

Reproduction is by means of transverse fission with or without the formation of catenula. In no case have chains of more than four individuals been observed while single specimens and pairs are much more common. No cysts have been seen, either in the small intestine with the vegetative adults or further back in the intestine.

SYSTEMATIC POSITION

From the foregoing it becomes clear that the present ciliate cannot be included in the genus *Haptophrya*; the neck, the small size and the rapid movement all set it apart from this genus. While these characters are suggestive of *Sieboldiellina* the absence of an alveolar ectoplasm, the presence of endoplasmic fibrils and the highly developed sucker all make such an identification unjustifiable.

On the basis of the characters observed it seems necessary to consider this organism as a representative of a genus new to science. For this genus I propose the name *Cepedietta* in recognition of the great contribution of Casimir Cépède who brought order into the chaos that was the Astomata.

Cepedietta nov. gen.

Genus of the family Haptophryidae without uncinus; constriction in the form of a neck; well developed sucker not bordered with long cilia; numerous contractile fibrils in endoplasm; dorsal contractile canal; size moderate.

Cepedietta fibrillata nov. gen.; nov. spec.

Species of the genus *Cepedietta* with the characters of the genus. Length. 500-700 μ ; dorsal part of "head" slightly prolonged anteriorly; neck occupies second seventh of body length; macronucleus large, alveolar, lacking chromatin spherules; no micronucleus recognized; endoplasm and ectoplasm sharply differentiated; contractile canal broad (28 μ); catenulation.

Locality: Oxford, Massachusetts.

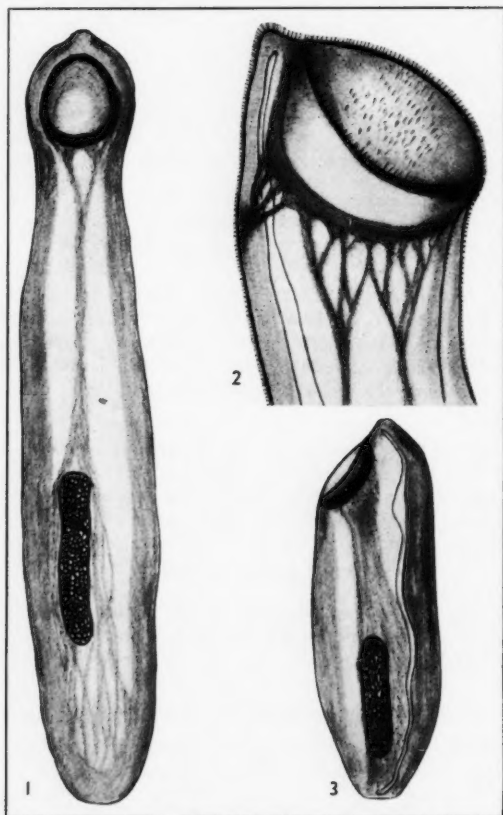
Host: *Eurycea bislineata* (Green).

Location in host: Small intestine.

Type: U. S. N. M. No. 36802.

SUMMARY

A new astomatous ciliate, *Cepedietta fibrillata*, which has affinities with the genera *Sieboldiellina* and *Haptophrya* is described from the intestine of the newt, *Eurycea bislineata*.



Figs. 1-3. *Cepedietta fibrillata* nov. gen., nov. spec. 1. Ventral view of entire animal, $\times 175$. 2. Side view of anterior portion showing attachment of contractile fibrils to the sucker, $\times 500$. 3. Side view of terminal member of a catenula, $\times 175$.

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Seasonal Distribution of Midge Larvae in a Senescent Lake*

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The seasonal distribution of certain limnologically important species of midge larvae, which seems to vary from one lake to another, is incompletely understood. During the course of an ecological study on the food-cycle dynamics of Cedar Bog Lake, Minnesota, the author has been able to assemble quantitative seasonal data over a four-year period on seven important species of lacustrine larvae. It has been found that neither quantitative observations on larval populations nor the periodic collection of adults alone is adequate to determine the seasonal distribution of these species. Recognizing this, the author in 1939 and 1940 attempted to combine the above methods, and also to rear under controlled conditions the larvae of certain species captured at various intervals.

Cedar Bog Lake is a shallow senescent lake about 35 miles north of Minneapolis; its developmental status and ecological composition have been described in preceding papers of this series (Lindeman, 1941a, 1941b). During the period from March, 1937, to March, 1941, quantitative seasonal collections of the bottom fauna were made with a modified Birge-Ekman dredge (225 cm²) from "open water," "pondweed" and "marginal" areas, respectively. The number of dredge samples taken on each date varied from 12 to 18 during the ice-free seasons, and 8 to 10 during the winter.

This paper summarizes the seasonal data for the seven most important midge species found in the lake: *Chironomus plumosus* Linnaeus, *Chironomus decorus* Johannsen, *Chironomus (Glyptotendipes) lobiferus* Say, *Chironomus (Endochironomus) nigricans* Johannsen, *Procladius culiciformis* (Linnaeus), *Palpomyia* sp. and *Chaoborus punctipennis* (Say). The many other species of midge larvae and adults which have been collected from Cedar Bog Lake during the course of this study have not been sufficiently abundant to give adequate indication of their general seasonal distribution.

CHIRONOMUS PLUMOSUS and CHIRONOMUS DECORUS

Chironomus plumosus, both Palearctic and Nearctic in its distribution, is perhaps the most important organism in the profundal regions of eutrophic lakes; it is also found in great numbers in ponds and sluggish ooze-bottomed streams. *Chironomus decorus*, apparently strictly Nearctic in distribution, is most abundant in shallow ooze-bottomed ponds and streams (Johannsen, 1937b). Both species are very tolerant of anaerobic conditions (Lindeman,

* This is the fifth of a series of papers, "Ecological Studies of a Senescent Lake," describing various ecological aspects of Cedar Creek Bog, Minnesota. Contributed from the Zoology Department of the University of Minnesota.

1942). The larvae of these two species are extremely similar in appearance, in ecological status and even in their anaerobic capacities, and are here considered together.

Remarkable annual species-substitution between these two forms was noted in the lake. An abundant population of *plumosus* alone, present in the winter of 1936, was completely replaced by a sparse population of *decorus* during 1937. A small population of both species was present in 1938, while in 1939 both species increased tremendously in numbers and importance. During 1940 the population of *plumosus* greatly declined, while that of *decorus* seems to have disappeared completely. Richardson (1921) commented on the discrepancies between the presence of great numbers of both *plumosus* and *decorus* in the Illinois River and their apparent inability to traverse by wing the short distances across timbered ridges to oxbow lakes which presented the same degree of pollution. In another paper (1928) Richardson gave tables showing the same sort of tremendous annual fluctuations for *plumosus* as are here reported, but attributed this at least in part to the effect of floods at mating time. While it seems not unlikely that unfavorable weather at mating time may have disturbed the natural reproduction in Cedar Bog Lake, no explanation can be given for this remarkable alternation of species.

Several summer generations of *Chironomus decorus* seem to develop each year in shallow warm-water habitats. Ping (1917, p. 425) reported evidence that probably five generations per year may develop in the vicinity of Ithaca, New York. Cultures of larvae from Cedar Bog Lake maintained at a temperature of 20° C. were observed to pupate and emerge within a few weeks. The data for 1937 (Table 1) indicate that probably several sparse generations of *decorus* were developing and emerging throughout the summer months. In 1940 the emergence of adult midges in Cedar Bog Lake was carefully observed at biweekly intervals. *Chironomus decorus* was the first midge species to emerge; numerous pupae were collected on iv-28-40, and on v-11-40 multitudes of adults were seen emerging from the surface. By v-26-40 (see Table 1) almost all of this species had emerged, as had many of *plumosus*. For unknown reasons *decorus* did not reproduce itself in the lake; 2 pupae were collected on vi-24-40, and one adult was reared from larvae collected on vi-7-40, but the species was not found in subsequent summer collections. These meager data, however, suggest that three generations of adults had emerged in 1940 between April and the end of July.

The emergence of *Chironomus plumosus* adults in Cedar Bog Lake was also studied at biweekly intervals during the spring and summer of 1940. The first emergents appeared late in May. The majority of larvae and pupae had emerged by vi-24-40, and many larvae of the next generation occurred in the dredgings of this date. A month later (vii-27-40) all larvae collected (61 from 10 dredgings, 2250 cm.²) were more than 18 mm. in length and averaged 25 mm. in length, indicating that all were members of a second generation of *plumosus*. Some of these larvae were cultured in the laboratory at 20° C., approximately the temperature of the lake ooze during this period, and

emerged as second-generation adults on VIII-28-40. In late September (IX-29-40) 10 dredgings yielded only 12 very large larvae (ca. 30 mm.); these larvae, cultured in ooze collected at the same time and kept at 20° C., emerged between Oct. 15 and Oct. 22. An adult *plumosus* was collected over the lake on Oct. 20, presumably a member of this same generation. Benthic collections on this same date (X-20-40) yielded only 4 last-instar larvae in 10 samplings, suggesting that a third generation of adults was emerging during late October. These same collections (X-20-40) also yielded small larvae 2-9 mm. in length. Samplings on XII-8-40 and III-28-41 indicated that very few of these small larvae were able to survive the winter, in contrast to the relatively high survival of the preceding winter. These data strongly suggest that three generations of *plumosus* reached maturity in this shallow senescent lake during 1940.

TABLE 1.—Seasonal Populations of *Chironomus plumosus* and *Chironomus decorus* in Cedar Bog Lake.

Numbers and moist weights (in grams) per square meter for the "open water" area.

Date	<i>Chironomus plumosus</i>		<i>Chironomus decorus</i>	
	Numbers	Weights	Numbers*	Weights
III-8-37	128	4.16
IV-26-37	97	3.74
V-25-37	72	3.05
VI-26-37	40	2.29	3	.005
VII-16-37	13	0.52	6	.008
VIII-20-37	74	.052
IX-15-37	62	.072
X-17-37	170	.611
XI-13-37	150	.507
II-26-38	118	.447
IV-3-38	66	.370
VII-30-38	13	.005
X-16-38	22	0.50	359	.300
XII-22-38	12	0.28	188	.140
III-4-39	40	0.83	33	.053
V-23-39	929	.24
VI-15-39	335	.37
X-15-39	95	1.45	775	.30
I-13-40	264	9.95	2000	3.20
III-3-40	204	9.40	1810	6.80
IV-28-40	87	3.50	661	2.10
V-26-40	29	0.69	2	.01
VI-24-40	306	5.83
VII-27-40	246	16.75
IX-29-40	53	2.12
X-20-40	13	0.70	67	.20
XII-8-40	26	0.75	60	.10
III-28-41	15	.06

* These numbers represent larvae smaller than 18 mm in length, and thus may include some indistinguishable immature larvae of *Chironomus plumosus*.

The life span of *Chironomus plumosus* as found in Cedar Bog Lake is quite different from that of this species in other types of habitats. In Lake Pepin, a deep lake-like enlargement of the Mississippi River between Minnesota and Wisconsin, this same species has two generations per year (Johnson and Munger, 1930). In large eutrophic lakes *plumosus* has only one generation per year (Grosser Plöner See, cf. Lundbeck, 1926; Lake Minnetonka, cf. Wood, 1938; Lake Waskesiu, cf. Rempel, 1936). The summer bottom temperature of Lake Pepin is doubtless lower than that of Cedar Bog Lake, while the bottom temperatures of the large eutrophic lakes mentioned are still lower, seldom more than 10° C. Scott and Opdyke (1941) reported that the number of summer insects emerging from the waters of eutrophic Winona Lake is much greater over shallow water than over deep, with a corresponding general but inexact association between greater emergence and higher bottom temperature. In Costello Lake, Ontario (Miller, 1941), shallow water species also emerged first from the shallowest and last from the deepest parts of their range. In explanation of this, Miller suggested that a longer time is necessary in the deeper part of their range to accumulate the day-degrees of heat energy required by the species. It therefore seems probable that the number of generations produced each year is likewise more or less directly proportional to the temperature of the ooze in which the larvae live. Such a conclusion is quite in accord with the generalized temperature-sum rule (cf. Bodenheimer, 1938), which states that the product of time and effective temperature (= environmental temperature minus development threshold) is constant.

The seasonal weight and frequency distribution of *plumosus* and *decorus* in Cedar Bog Lake during the fall and winter of 1939-40 (Fig. 1) may profitably be compared with that given by Lundbeck (1926) for *plumosus* and *liebeli-bathophilus* (the latter seems analogous to *decorus* in America) for Plöner Becken, Germany (Fig. 2). The two diagrams are quite similar except for the late winter and spring periods.

The deleterious effects of extended winter conditions are shown in both figures. In Cedar Bog Lake, where the period of anaerobiosis was definitely known, subjection of the forms to 50 days of oxygen-free conditions took a rapid toll, and affected *plumosus* (43% survival) less seriously than *decorus* (38% survival, cf. Lindeman, 1942). While the late winter period in Cedar Bog Lake showed devastating reduction in numbers, the corresponding period in Grosser Plöner See is represented (Fig. 2) as conducive to rapid growth. An explanation for this great difference is suggested by facts recorded in an earlier portion (p. 95) of Lundbeck's paper. During February of 1924, very mild weather combined with high winds resulted in melting of the ice on Plöner See for a time. The water doubtless underwent premature warming and circulation; very probably this change accounted for the pre-vernal *Chironomus* growth he reported, assuming that his meager samplings were adequate. Lundbeck reported a similar pre-vernal growth effect the following year, but gave no data as to the lake conditions at that time. The larger lakes of that region, according to his data, appear to be normally ice-bound from

mid-December until late March. That such a distinct individual weight increase should take place in the spring, simultaneously with complete circulation of the lake and a rise in temperature, is not unexpected, but that such an increase should occur before the usual time of ice-disappearance seems quite incredible. Lundbeck's curve would better conform to the expected type if the vernal increase in growth would follow rather than precede the spring break-up of ice. The corresponding vernal rise in the Cedar Bog Lake is masked by the emergence of *Chironomus decorus*.

Fig. 1.

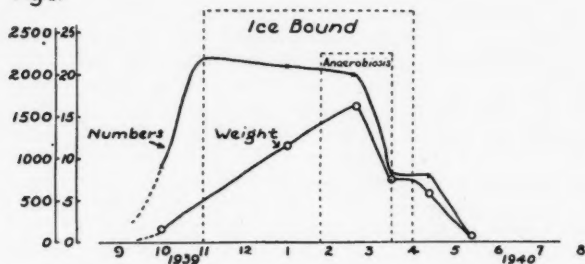


Fig. 2.

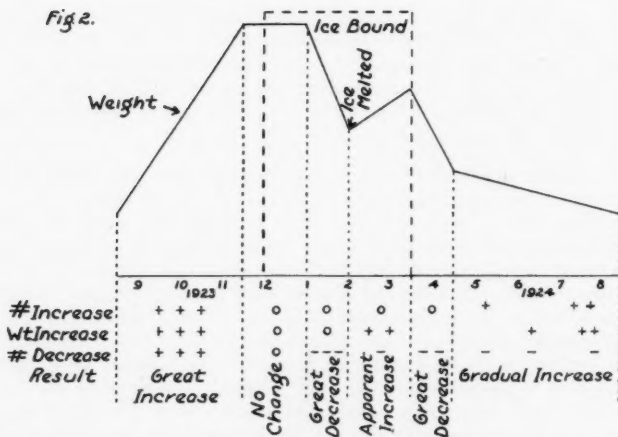


Fig. 1. Annual frequency and weight curves for *Chironomus plumosus* + *C. decorus* in Cedar Bog Lake, Minnesota. Numbers and moist weight (in grams) per square meter. (Cf. Table 1).

Fig. 2. Annual weight curve for *Chironomus plumosus* + *C. liebeli-bathophilus* in Grosser Plöner See, Germany (after Lundbeck, 1926).

The spring emergence of adults in Grosser Plöner See (Lundbeck, p. 213) showed that the smaller species, *Chironomus liebeli-bathophilus*, emerged earlier than *plumosus*. Lundbeck believed that emergence in the case of the former species was due to the ecological factor of rising temperature, and that in the case of *Chironomus plumosus* emergence was due to the onset of summer stagnation with lowering of the benthic oxygen tension. This same factor was suggested for *plumosus* by Rempel (1936) in Waskesiu Lake of Prince Albert Park, Saskatchewan. Lundbeck did admit certain exceptions to this rule in other lakes but explained these as due to differences of lake typology. Certainly the emergence of *plumosus* in Cedar Bog Lake and in Lake Pepin (Johnson and Munger, 1930) was not due to the onset of summer anaerobiosis; Lundbeck's and Rempel's explanation, therefore, is probably not the "determining factor" for the emergence of adults. It seems more probable that larval growth is largely a function of temperature, and that when growth is completed (the water being above some threshold temperature), pupation and emergence follow.

In summary, great fluctuations and species-substitutions occur in the Cedar Bog Lake populations of *Chironomus plumosus* and *Chironomus decorus*. The former species may have as many as three generations per year in this lake, and the latter may have even more. Both species occupy the same ecological niche in relation to the metabolism of the lake. The number of generations per year is believed to depend upon the temperature of the benthic ooze.

CHIRONOMUS (GLYPTOTENDIPES) LOBIFERUS

The important subgenus *Glyptotendipes* is represented in Cedar Bog Lake by *Chironomus lobiferus*. The larvae of at least some members of this group burrow in the submerged parts of aquatic plants. Three species of this subgenus, *lobiferus*, *barbaris* and *paripes*, are known for Minnesota, according to the Minnesota Entomology Museum specimens identified by Dr. H. K. Townes in 1938. Adults reared from Cedar Bog Lake larvae correspond most closely to *lobiferus*, although the adults are separated on what seem to the writer to be relatively minor characters. *Chironomus lobiferus* is Nearctic in its distribution. The larvae of this species have been reported from very antagonistic extremes of habitat types, ranging all the way from the sandy beaches of Lake Mendota (Muttkowski, 1918) and shallow prairie lakes of Minnesota (Wilson, 1938) to polluted backwaters of the Illinois River (Richardson, 1928) and the tenuous ooze of Cedar Bog Lake. One or two morphological features of the Cedar Bog Lake larvae are noteworthy: the size is greater than is usually indicated for the species, and the ventral gills on the eleventh segment are definitely vestigial, mere "lobes." These larvae were found to be most numerous in the pondweed and marginal areas, where the ooze is less tenuous than in the deeper areas.

The general seasonal distribution of *lobiferus* in Cedar Bog Lake is indicated in Table 2. In 1937 at least one summer brood developed in the marginal area, where large larvae and pupae were collected in July and August, with

smaller larvae again in September. A period of emergence during October is also suggested, although no pupae were found. Relatively small populations were present in 1938, but by 1939 the species was again more abundant. In the early summer of 1940 observations on emergents were made at biweekly intervals. The overlapping larvae of 1940 grew rather rapidly following the spring thaw, so that by late May adults were emerging in great numbers. On May 26 thousands of exuviae were floating on the surface; 100 of these were collected and measured as an index of size variation. Johannsen (1937b) indicated the pupal length as 9 mm., but the Cedar Bog Lake forms were much larger, ranging from 9.5 to 13 mm. in length; and the mean length, based on 100 specimens, was 11.2 ± 0.0085 mm. One month later (vi-24-40) myriads of tiny larvae (ca. 2 mm. long) were collected in the dredgings, particularly in the pondweed zone, although some mature larvae and a few pupae were still present. By July 27 these tiny larvae had become a large population of mature and semi-mature larvae all over the lake bottom. From

TABLE 2.—Seasonal Populations of *Chironomus lobiferus* in Cedar Bog Lake.
Numbers and moist weights (in grams) per square meter.

Date	Open Water Area		"Pondweed" Area		Marginal Area	
	No.	Wt.	No.	Wt.	No.	Wt.
III-28-37	3872	35.95	13398	54.82	*	*
IV-26-37	1254	16.46	3036	19.70	183	1.26
V-25-37	132	.57	726	4.31	4263	19.64
VI-26-37	1506	6.80
VII-16-37	44	.06	100	.10	6028	13.04
VIII-20-37	1422	3.01
IX-15-37	1000	.39
X-17-37	1906	4.27
XI-13-37	88	.04	783	2.06
II-26-38	33	100	.04	*	*
IV-3-38	1133	3.28
VII-30-38	511	.86
X-16-38	11	.01	286	.61	1578	4.40
XII-22-38	132	.04	66	.38	*	*
III-4-39	66	.04	*	*
V-23-39	11	.05	22	.01	183	.35
VI-15-39	902	.27	†	†
X-15-39	77	.26	396	.66	1510	1.78
I-13-40	736	1.76	*	*
III-3-40	11	.01	480	.69	*	*
IV-28-40	18	.07	409	1.61	2468	15.77
V-26-40	18	.15	204	1.25	3055	14.42
VI-24-40	1225	.41	12830	9.65	5010	4.11
VII-27-40	1291	4.26	2455	4.62	1145	.51
X-20-40	337	.11	169	.08
XII-8-40	*	*
III-28-41	*	*

* Marginal areas frozen solid in winter; no collections made.

† No quantitative collections made in marginal area on this date.

ooze samples of this date cultured at 20° C., numerous adults emerged during August. On September 1, several adult *lobiferus* of this second generation were captured over the lake. Although no regular sampling of the benthos was made in September, an extremely sparse population of tiny larvae was present on October 20; these apparently represented the offspring of a third generation. In marked contrast to the previous winter, the species was practically absent from samples collected in the winter of 1940-41.

Chironomus lobiferus is thus seen as a very irregular, but occasionally important, member of the ooze fauna of Cedar Bog Lake. It becomes most abundant in the pondweed and marginal areas, and apparently develops three generations per year.

CHIRONOMUS (ENDOCHIRONOMUS) NIGRICANS

The subgenus *Endochironomus*, represented in Cedar Bog Lake chiefly by *Chironomus nigricans* Johannsen, occurred in considerable numbers among

TABLE 3.—Seasonal Populations of *Chironomus nigricans* in Cedar Bog Lake. Numbers and moist weights (in grams) per square meter.

Date	Open Water Area		"Pondweed" Area		Marginal Area	
	No.	Wt.	No.	Wt.	No.	Wt.
III-29-37	*	*
IV-26-37	22	.01
V-25-37
VI-26-37	33	.07
VII-16-37	143	.19	165	.13	1367	.60
VIII-20-37	66	.02	374	.18	133	.09
IX-15-37	154	.04	308	.08	67	.06
X-17-37	11	.01	483	.19
XI-13-37	33	.02
II-26-38	*	*
IV-3-38	132	.06	100	.12	350	.18
VII-30-38	33	.02	121	.17	1161	.59
X-16-38	11	.01	847	.48	4767	2.52
XII-22-38	*	*
III-4-39	*	*
V-23-39	11	.01	22	.01	6667	2.06
VI-15-39	†	†
X-15-39	11	.02	88	.22
I-13-40	9	.01	*	*
III-3-40	*	*
IV-28-40	89	.04	71	.08	4850	3.03
V-26-40	18	.06	9	.01	611	1.23
VI-24-40	9	.01	71	.08	389	.40
VII-27-40	18	.01
X-20-40	1511	1.06
XII-8-40	36	.02	*	*
III-28-41	*	*

* Marginal areas frozen solid in winter; no collections made.

† No quantitative collections made in marginal area on this date.

and beneath the pondweeds just off the marginal mat. Members of this subgenus are believed to have little resistance to anaerobic conditions; no larvae could be found in late winter collections (Table 3). It may be that the Cedar Bog Lake species overwinters in the egg stage. In the lakes of Japan, Miyadi (1932, p. 137) found that *Endochironomus* larvae occurred abundantly on deeper bottoms where dissolved oxygen was present, but were few or limited to shallow bottoms in those lakes in which the deep water contained little or no oxygen. Miller (1941) found this species in the non-anaerobic hypolimnion of Costello Lake, Ontario, where he suggested that it requires two years to reach maturity.

The seasonal distribution of *Endochironomus* larvae in Cedar Bog Lake is indicated in Table 3. Larvae first appeared in late April and persisted through the warm summer months until October. The data for 1937 suggest the presence of three generations of larvae. The 1938 and 1939 data are too infrequent to show seasonal generations. The summer samplings in 1940 appear to have missed a generation. Primarily on the strength of the 1937 data, this species is believed capable of developing three generations per year in Cedar Bog Lake.

PROCLADIUS CULICIFORMIS

Procladius culiciformis, an important ooze predator in eutrophic lakes, is "a cosmopolitan species widely distributed in the United States" (Johannsen, 1937a). In Lake Minnetonka, the species was found to be fairly evenly distributed from depths of 4 meters to 15 meters (Wood, 1938), but only a few individuals were found in the deepest profundal areas at 24 meters. Miller (1941) found this species at all depths (1-17 meters) in Costello Lake, Ontario, but more abundant in shallow water. In the senescent Cedar Bog Lake, a sparse *Procladius* population occurred over all parts of the bottom.

Concerning the seasonal distribution of *Procladius*, Johannsen (1937a) states that "the larvae hibernate when they are half grown," implying one generation per year. A similar distribution is reported for *Procladius culiciformis* in Costello Lake by Miller (1941), where emergence began late in June and lasted until early August. In explanation of a more or less simultaneous emergence from shallow and deep water, he suggested that individual larvae of this and a closely related species migrate back and forth through the thermocline, "each moving from one depth to another at random, and, consequently, each receiving the same amount of heat." The data from Third Sister Lake, Michigan (Eggleton, 1931) present a somewhat different picture: when the benthos population figures for depths from 7 to 15 meters are averaged together and plotted into a seasonal curve (Fig. 3), a definite suggestion of bimodality is attained. Although Eggleton records no values for March, it seems safe to assume that the population rise did not begin until after the spring thaw in late March, as indicated by the broken line. These seasonal figures are based upon a sufficient number of collections to minimize errors of sampling. Tables from a seasonal study of Lake Minnetonka by Miss Evelyn Wood (1938), whom the author assisted with field collections, indicate a *Procladius* population numerically comparable with that of Third

Seasonal Frequency Distributions of *Procladius californicus*.

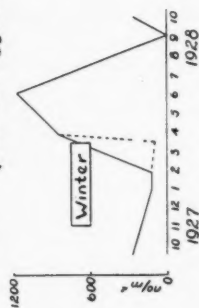
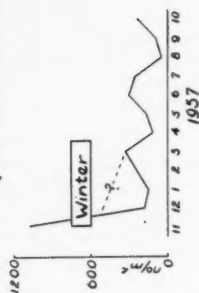
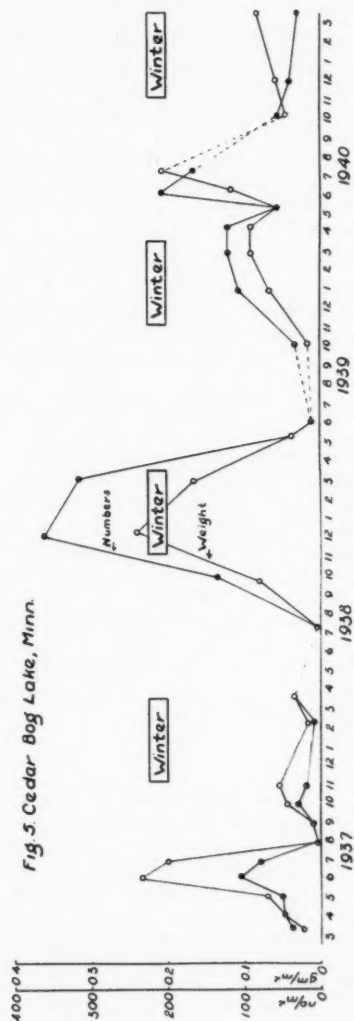
 Fig. 3. Third Sister Lake, Mich.
(data from Eggleton, 1931)

 Fig. 4. Lake Minnetonka, Minn.
(data from Wood, 1938)


Fig. 5. Cedar Bog Lake, Minn.



Sister Lake. To obtain the data plotted in Fig. 4, Wood's figures for populations at depths of 4, 6, 10 and 15 meters were averaged; this represents sampling areas of at least 4 square feet (4 Peterson dredge samples) for each month of the winter, and somewhat more than this for summer samplings. The midwinter sag in the curve suggests a sampling defect probably correlated with extremely inimicable collecting conditions. Her summer data clearly suggest a second midsummer generation. It is interesting that the Minnetonka curve is almost the complement of that for Third Sister Lake, substituting winter for summer population peaks. Moffatt (1942) has recently reported that two generations of *Procladius culiciformis* develop per year in the littoral areas of Douglas Lake, Michigan.

The seasonal *Procladius* curves for Cedar Bog Lake are plotted in Fig. 5 as numbers and moist weights of the larvae. The collections during the winter of 1936/1937 show marked small-sampling effects, emphasized by the scant population; the curve has hence been arbitrarily drawn as the mean of all samples during that winter. The figures for the remainder of 1937, though still statistically objectionable, are very interesting: emergence of some large larvae just after the spring breakup is suggested, followed by an increase in numbers of small larvae, a rapid growth to maturity during June and July with emergence of the entire population before mid-August; small larvae were again found during late autumn, and these over-wintered beneath the ice. Incomplete data for the following year suggest a recurrence of this cycle, with larvae overwintering at a much smaller size; this seems to have disrupted the procedure for the 1939 season so that perhaps (serotinal data were unfortunately not collected) the summer brood did not develop during that year. The data for 1940 present a definitely bimodal curve, with the possible insertion of an additional midsummer generation in August and September. In general, these data suggest at least two generations per year of *Procladius culiciformis* in Cedar Bog Lake. The data from these various lakes indicate that *Procladius culiciformis* normally has two generations per year in the lakes of this region.

PALPOMYIA sp.

The vermiform larvae of the *Ceratopogonidae* are mostly littoral forms associated with beds of pondweeds and blanket algae. A very few forms may be found in profundal ooze of eutrophic lakes, but even these are wanderers from concentration zones of the same species in shallower water. Several species of the vermiform "*Palpomyia* group" of *Ceratopogonidae* occur in the Cedar Bog Lake. The most abundant member of this group is a species much resembling larval descriptions of *Palpomyia tibialis*, but which because of its size has been called here *Palpomyia* sp. This form seems well adapted to the tenuous ooze environment, and on the basis of winter survival experiments (Lindeman, 1942) it appears able to withstand anaerobic conditions as well as does *Chironomus plumosus*. Mayer (1934) indicates that such larvae are very resistant to freezing, and quotes other authors as having found them in frozen ponds.

The literature seems to contain very little data on the life histories of this group, although many forms have been reared to adulthood in captivity. The best paper encountered which included life history data was by Rieth (1915), but even this limited itself to a mention of dates when the various stages were found in different localities. His data suggested that *Palpomyia* adults emerge in May, and that *Bezzia* adults occur from the beginning of June to the middle of August. Thomsen (1937), who studied the metamorphosis of many species near Cornell University, reported finding pupae of *Palpomyia* at the edge of a pond "in mid-summer." She also reported for *Bezzia varicolor* (p. 78) that "the developmental period from egg to adult averages two months." Speaking of these forms in general, Muttkowski (1918, p. 408) reported that "they pupate in July." Such information does not shed much light on the problem at hand.

The population data for Cedar Bog Lake from 1937 to 1940 are shown in Table 4. It seems evident that during those years when summer collections were frequent (1937 and 1940) this species developed at least two genera-

TABLE 4.—Seasonal Populations of *Palpomyia* species in Cedar Bog Lake. Numbers and moist weights (in grams) per square meter.

Date	Open Water Area		"Pondweed" Area		Marginal Area	
	No.	Wt.	No.	Wt.	No.	Wt.
III-29-37	396	1.80	550	2.20	*	*
IV-26-37	176	1.19	231	1.52	56	.01
V-25-37	88	.44	66	.37	167	.98
VI-26-37	44	.13	44	.11	50	.21
VII-16-37	44	.26	33	.13	22	.09
VIII-20-37	11	.03	72	.16
IX-15-37	11	.03	55	.18	33	.07
X-17-37	11	.04	39	.17
XI-13-37	22	.08	83	.26
II-26-38	11	.04	11	.04	*	*
IV-3-38	55	.19	22	.06	44	.10
VII-30-38	6	.01
X-16-38	583	.93	814	1.65	39	.08
XII-22-38	528	.88	1540	2.36	*	*
III-3-39	517	1.10	275	.44	*	*
V-23-39	550	.44	143	.12	367	1.21
VI-15-39	143	.15	297	.31	†	†
X-15-39	110	.37	187	.69	356	.27
I-13-40	213	.55	115	.29	*	*
III-3-40	278	.94	160	.56	*	*
IV-28-40	124	.21	187	.83	94	.35
V-26-40	71	.51	116	.27	494	2.86
VI-24-40	53	.11	532	.94	22	.04
VII-27-40	198	.84	303	.95	155	.39
X-20-40	231	1.29	472	1.68	155	.33
XII-8-40	312	1.53	1040	4.45	*	*
III-28-40	244	.80	177	.53	*	*

* Marginal areas frozen solid in winter; no collections made.

† No quantitative collections made in marginal area on this date.

tions; collections during 1938 and 1939 were too infrequent to be of value. The adults emerge in early June. On vi-9-40 great numbers of pupae were floating at the surface near the margin. Large larvae of the second generation were collected in considerable numbers on vii-27-40. Large larvae were also collected on ix-1-40 and emerged in about two weeks when cultured in ooze from the lake maintained at 20° C. Great numbers of various-sized larvae were found on x-20-40, at least some of which were probably offspring of the September (third) generation. These data indicate that the species of *Palpomyia* develops two, and perhaps three, generations per year.

CHAOBORUS PUNCTIPENNIS

The species of *Chaoborus* found in Cedar Bog Lake, *Chaoborus punctipennis*, is widely distributed over the lake-states of North America, and is the species most commonly reported from lacustrine benthos. The genus is still widely known by the former name of *Corethra*.

Fortunately for our purpose, considerable data have been collected on the seasonal distribution of this species for two eutrophic lakes in nearby regions: Lake Mendota, Wisconsin (Juday, 1922), and Third Sister Lake, Michigan (Eggleton, 1931). Seasonal data on *Chaoborus flavicans* from Esrom Lake, Denmark, are also available (Berg, 1937). Seasonal curves of *Chaoborus* in the profundal benthos of these lakes, together with the curve for Cedar Bog Lake, are plotted comparatively in Figs. 6 to 9.

The normal seasonal distribution of stabilized *Chaoborus* populations in the profundal zones of Third Sister Lake and Lake Mendota, two quite different types of eutrophic lakes, is shown in Figs 6 and 7. The generalized seasonal curves for *Chaoborus* in these two lakes are similar: very high larval populations built up in late autumn are slightly decreased during the winter and very rapidly decreased in the spring as a result of pupation and emergence of adults; following this initial spring decline, the population declines gradually to an August minimum, after which the autumnal rise again becomes apparent. Muttkowski (1918) suggested the existence, in Lake Mendota, of two rapid summer generations in addition to the over-wintering one. The different curve gradients for the two lakes are perhaps due to a more rapid response to seasonal temperature changes in the smaller lake.

The periodicity of *Chaoborus* was discussed in some detail by Berg (1937). He maintained that in the large Esrom Lake but one generation of *Chaoborus flavicans* (Fig. 8) is produced each year, with the adults emerging in "swarms" during mid-July. In shallower Frederiksborg Castle Lake two generations seemed apparent. Meinert (1886) believed that two generations could be produced per year, as did also Frankenberg (1915). Lundbeck (1926) reported a one-year cycle for *Chaoborus plumicornis* in Pluss-See, as did also Miyadi (1932, p. 130) for the Japanese "*Corethra*-lakes."

The Cedar Bog Lake curve, as indicated by the data for 1939-1940 (Fig. 9), shows a different seasonal pattern from that of the other lakes. An October maximal population of 43,726 individuals per square meter for the open water area (20,108 for the lake as a whole) gradually declined during the late fall and

Seasonal Frequency Distributions of *Chaoborus punctipennis*.

Fig 6 Lake Umbagog, N.H. (data from July, 1917)

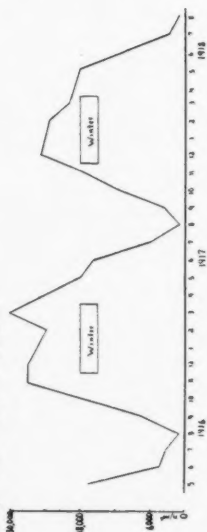


Fig 8 Euxine Lake, Rouman (data from Aug. 1919)

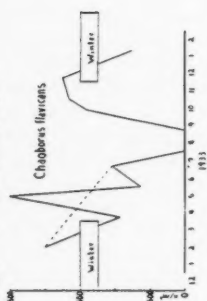


Fig 7 Third Sister Lake, Mich (data from September, 1919)

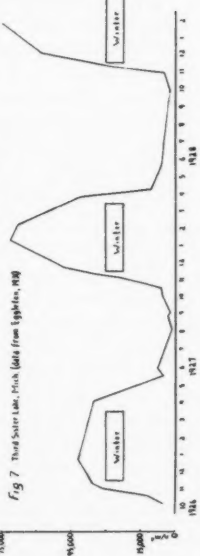
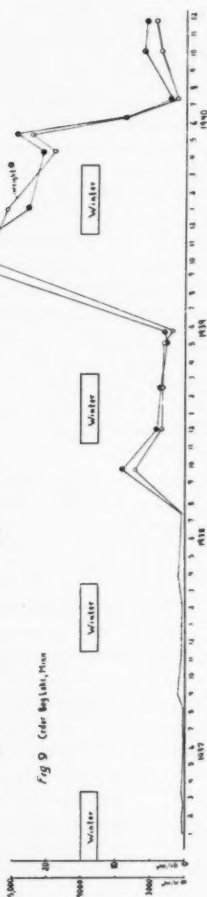


Fig 9 Cedar Bay Lake, Minn



winter, affecting numbers more strikingly than size; this suggests the possibility that the population decline was caused primarily by starvation and that the larger larvae may have cannibalistically devoured the smaller individuals (cf. Meinert, 1886, p. 409).

The possibilities of faulty winter sampling were studied, primarily for the purpose of determining any phototropic effects which might follow the cutting of a "window" through the curtain of ice and snow over the lake. For this reason the collections of I-13-40 were taken by two techniques, seven collections taken immediately upon cutting holes through the ice, and three collections taken more than an hour after cutting the holes. The data showed no evidence of either positive or negative phototropism. No further regard for this factor was believed necessary for the two following winter series (March 3 and 30), and on these dates the holes were opened some time before dredging so that plankton and chemical samples could be taken. Upon analysis of the benthic counts, however, the author was astonished to find a great increase over the expected numbers, consisting mostly of large larvae, as indicated by their weight values. In searching for an explanation of such obvious sampling errors, it was noticed that at the time "controlled samplings" were made on Jan. 13, dissolved oxygen was abundant beneath the ice (12.0 ppm.), while on the subsequent winter sampling dates anaerobic conditions prevailed. This strongly suggests that on the latter dates large individuals were responding to the slight amount of oxygen entering the water during the interval between cutting of the holes and the taking of benthos samples. Just why more of the larger larvae should respond in this fashion is still unknown. Because of this phenomenon, the values for III-3-40 and III-30-40 in Fig. 9 are not considered to be valid.

The population changes in Cedar Bog Lake during the spring of 1940 suggest a small emergence of adults shortly after the spring break-up, as a few tiny larvae occurred in the IV-28-40 samples; these small larvae were joined by others during May, while the main mass of older larvae were accompanied by numerous pupae, causing a secondary rise in the seasonal curve for V-26-40. It is not inconceivable, however, that the early spring brood of young larvae might have hatched from over-wintering eggs laid the preceding fall; no adults were collected in marginal sweeps on IV-28-40 and no pupae occurred in the bottom samples. During June a great emergence of adults occurred, coincident with marked growth of the young larvae. By late July the benthic population had become minimal, consisting of a general mixture of small and large larvae, as well as pupae which may well have developed from eggs laid during the same summer. It should be emphasized that collections taken from May through September contained mixed sizes of larvae as well as pupae. No quantitative samplings were analyzed during August or September, but by October the population, particularly of smaller forms, had considerably increased; on the basis of larval development in experimental aquaria, it is believed that at least some of these small larvae were offspring of a third generation of adults which had emerged during September (cf. Berg, 1937, p. 25). These data indicate that *Chaoborus punctipennis* may develop several over-lapping generations per year.

Annual changes in the Cedar Bog Lake *Chaoborus* population (Fig. 9), unexplained at the present time, are rather startling, and seem to follow great fluctuations in the food-cycle dynamics of the lake. During 1936 and 1937 the *Chaoborus* fauna was very small, perhaps correlated with low water level. Beginning in the autumn of 1938 the population increased continually until the summer of 1940; by autumn (1940) the water level was again low, as was also the population of *Chaoborus*.

Summary

1. A four-year study of Cedar Bog Lake, a senescent eutrophic lake in Minnesota, revealed striking annual and seasonal changes in the populations of midge larvae.

2. *Chironomus plumosus*, *Chironomus decorus*, *Chironomus lobiferus* and *Chironomus nigricans* were found to develop three generations per year.

3. *Procladius culiciformis* and an undetermined species of *Palpomyia* were found to develop at least two, and probably sometimes three, generations per year.

4. *Chaoborus punctipennis* was found to develop several over-lapping generations per year.

5. Temperature seems to play a primary rôle in determining the seasonal distribution of midge larvae and the number of generations developed per year. Midge larvae living in the cold profundal ooze of deep eutrophic lakes usually have but one generation per year, while in the warm ooze of the shallow senescent lake here studied, these species have additional generations produced during the summer months. These conclusions are in agreement with the temperature-sum rule of insect development.

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The Centers of Distribution of the Chaparral and Coastal Sage Associations

Carl Epling and Harlan Lewis

Introduction

The vegetation of cismontane Southern California consists chiefly of three well defined communities of different aspect and habit: the oak woodland, the chaparral and coastal sage associations. The first of these, as its name implies, is a woodland whose principal component is *Quercus agrifolia*, with which are variously associated such species as *Q. Engelmannii* and *Juglans californica*. This woodland is for the most part poorly developed in Southern California, where it appears to be relictual, chiefly occupying small valleys and potreros, on moister hillsides. It is surrounded and in many places all but engulfed, by the chaparral and coastal sage. It reaches its typical development in West Central California and may be interpreted there as a coastal expression of the oak woodland of the Great Valley. It extends southward as far as Santo Tomas in Baja California. We are concerned only indirectly with it here.

The chaparral and coastal sage communities are the characteristic and widespread associations of the area under discussion. They are not confined to Southern California, however. The former ranges in typical form into the North Coast ranges, being widely developed in Lake County and in corresponding latitudes in the Sierran foothills. It reappears in Central Arizona into which region at least three California species extend, and again, according to Muller (1939, and personal communication) in Chihuahua, Coahuila, and Nuevo Leon. Its aspect there is "strongly suggestive of California chaparral, as described by Cooper." Although several generic representatives are found common to both areas, such as *Quercus*, *Ceanothus*, *Cercocarpus*, *Rhus*, *Arctostaphylos*, and *Garrya*, the species differ, with the chief exception, perhaps, of *Arctostaphylos pungens*. Whether that species is actually common both to Nuevo Leon and to Southern California may be open to question. In any case, closely related phylads are represented, not only by *Arctostaphylos*, but also probably by *Cercocarpus*, *Garrya*, and *Ceanothus*. The scrub oaks of the Nuevo Leon association are not of the *Quercus dumosa* phylad, however, but are predominantly semi-deciduous oaks of Mexican alliance. According to Muller, it would appear that, although it has much the same aspect and habit, the chaparral of Nuevo Leon and Coahuila is a more diversified community than the chaparral of California, that is, harbors more elements which in California are found in other associations, as for example, *Agave*, *Nolina*, *Juniperus*, *Pinus cembroides*, *Mahonia Fremontii*, and *Arbutus*. In Nuevo Leon some of these elements, for example, *Pinus*, *Juniperus* and *Arbutus*, are not restricted to the chaparral, but occur freely and in true form in the adjacent forest types. As one proceeds westward, according to Muller, the

composition of the Mexican chaparral approximates more nearly to the Californian. In that of Coahuila, for example, is found such a species as *Ceanothus Greggii*, which does not penetrate to Nuevo Leon.

The chaparral climax has been defined by Cooper (1922) as:

A scrub community, dominated by many species belonging to genera unrelated taxonomically, but of a constant ecological type, the most important features of which are the root system, extensive in proportion to the size of the plant, the dense rigid branching, and pre-eminently the leaf, which is small, thick, heavily cutinized and evergreen.

The matrix of this community is *Adenostoma fasciculatum*. Throughout the range indicated, it may form extensive areas, pure in stand, or may be associated with the various species indicated below. These sometimes form extensive mixed stands from which *Adenostoma* is nearly excluded, of sufficient height in some places as to form approximately a low woodland beneath the canopy of which it is possible to push one's way erect. On other slopes, one or more of these species may be scattered through the *Adenostoma*, or may form small colonies within it.

The distant aspect of this vegetation is fairly uniform throughout the year because of its evergreen habit and even height. It is usually dark-green or olivaceous, particularly in late summer and autumn when the dried flowers and numerous small capsules of *Adenostoma* give a brownish tinge to its surface. Its density is such as to make penetration slow and difficult and produces the appearance of a dark, velvety mantle over the hills which it occupies.

Coastal Sage

The coastal sage community has a distribution similar to that of the chaparral but does not occur outside of California and is confined there chiefly to coastal areas and at lower elevations than the chaparral. It is preclimatic to the chaparral and intricately associated with it. It ranges in typical form from the Bay Region of central California southward to Rosario in Baja California. Its most widespread component species is *Artemisia californica*, which plays a rôle comparable to that of *Adenostoma* in the chaparral. Various associated with this widespread species are others of similar habit, such as *Salvia mellifera*, *S. apiana*, *S. leucophylla*, *S. Munzii*, *S. Brandegei*, *Eriodictyon crassifolium*, *E. sessilifolium*, *Viguera laciniata*, *Encelia californica*, *Lotus scoparius* and *Eriogonum fasciculatum*. *Artemisia californica* may form a pure or nearly pure stand, particularly in maritime situations, whether it be in Monterey County or far southward near San Quentin. It is more commonly associated with one or more of the species indicated above. On many slopes two or more of these species may be dominant, almost to the exclusion of any others.

To what extent these varied communities are "normal" is uncertain. The partial occupation by man of the natural terrain of both the chaparral and coastal sage has greatly modified their relative distribution and actual composition, especially by fire. We are indebted not only to our own observations, but also to Mr. Frank Gander, for the information that the coastal sage has invaded

and is successfully holding large areas which would normally support chaparral. If the severity of the fire is such as to prevent the stump sprouting which is characteristic of many chaparral species, it appears to be difficult for those species to regain control by seeding, particularly in critical areas.

The habit of the coastal sage is characteristically herbaceous or half-woody. Only in rare instances, these principally maritime, as at San Quentin, is the spacing such as to form a dense cover through which penetration is difficult. It rarely rises higher than a man's shoulders and ordinarily can be traversed without difficulty. Its reaction to drought is notably different from that of the chaparral. The soft leaves, as of the various species of *Salvia*, curl and wither as the summer progresses. The stems may even become bare and die back to some extent or other under more severe conditions of drought. The flowering branches commonly die back, becoming brown and sere. Because of the white pubescence which characterizes many of its species, such as the *Salvias*, *Eriodictyons*, and *Artemisia*, its aspect in spring and early summer is generally a gray-green which resembles that of the Great Basin Sagebrush. Its aspect in late summer and autumn, after the summer drought has wrought its effect, is a greyish brown, which may even verge to russet where the dried clusters of *Erigonum* are abundant. Because of the emphasis given by its spacing, it then resembles the *Larrea-Franseria* community of the Colorado desert, giving a pepper and salt aspect to the arid hills which it occupies.

That the ecological relationship between the chaparral and coastal sage is close may be deduced not only from their intimate and even intricate spatial relationships in disturbed areas, but also by the inclusion within each of species which are allied in ecological habit to the other type. For example, the chaparral of San Diego County may regularly include in some areas such species as *Salvia Clevelandii* or *S. sonomensis*, the latter ranging sporadically far northward, or *Trichostema Parishii*, or *Chamaebatia australis* which although definitely woody, has soft leaves which wither and turn brown as the summer progresses. On the other hand, the coastal sage may include such species as *Rhus ovata*, typically chaparral, woody and evergreen, although it is not always certain whether the ground occupied by such a mixture is permanently held by the coastal sage.

In northern Baja California this association of woody evergreen species is more pronounced. In that region they belong to genera which are not typically components of the chaparral, such as *Fraxinus trifoliata*, *Aesculus Parryi*, *Cneidium dumosum*, *Tetracoccus dioicus*, and *Simmondsia californica*. Some, such as the latter, are typical components of the *Larrea-Franseria* association. Others suggest relationships further south on the Mexican mainland. These species do not seem to form an integral part either of the coastal sage or the chaparral as it is developed in coastal areas there, but seem to hold themselves somewhat apart, as though strangers never fully accepted by the inhabitants. The effect of fire renders determination of their status additionally difficult. It is possible that in the inaccessible foothills of the Sierra Jaurez and Sierra San Pedro Martir, these species are more regularly associated with the chaparral.

Shreve (1936) in his treatment of the transition from desert to chaparral, in Baja California, seemingly considers the coastal sage to be either simply one aspect of chaparral or a transition vegetation. Perhaps this is only a question of nomenclature; perhaps it is the presence of the woody species referred to in the preceding paragraph which suggests this view. In any case it is a view difficult to accept. The marked differences in relation to drought of the main body of chaparral and of coastal sage, their spatial and altitudinal relationships, their successional relationship, the marked differences in floristic composition, all suggest two fairly well defined vegetational elements.

In a broad sense it is true, as he says, that the "trend of change in vegetation between Rosario and the Boundary is away from the characteristics of the desert and toward those of chaparral." The chaparral, chiefly chamisal (*Adenostoma fasciculatum*) at that latitude, persists southward as far as the Rio San Antonio along the coast. But the transition species from the Viscaïno desert, which he lists, are not associated with this chaparral or but rarely. They occur with the coastal sage, particularly on the llanos which stretch northward from Rosario to the Rio San Antonio and beyond. Such a transition area is pictured by Shreve. Further north than the area pictured but bearing the same aspect, the basic vegetation of the llanos is the coastal sage with such species to be expected as *Salvia Munzii* (vicarious here to *S. mellifera*), *Artemisia californica*, *Eriogonum fastigiatum*, *Viguera laciniata*, *Encelia californica* and *Eriodictyon sessilifolium*, with occasional individuals of *Aesculus Parryi*.

Historical Development

Axelrod (1939, 1940 abc) has demonstrated the historical relationship of the chaparral and oak-woodland communities and has traced their common origin in a generalized oak savanna which emerged from the north Mexican plateau during the Miocene, or earlier, and "by the end of that epoch had migrated westward into southern and central California and northward through the Great Basin." He has concluded that the chaparral as a vegetational element was probably evolved in Southern California since Pliocene time and suggests also that a definite historical relationship with the chaparral of central Arizona probably exists. The appearance in Nuevo Leon of *Rhus trilobata*, *Mahonia Fremontii*, and *Arctostaphylos pungens*, all found in the chaparral of California, suggests also a relationship with the chaparral of that area. This is also suggested by the presence of fossil counterparts of *Mahonia Fremontii* in the Tehachapi, Esmeralda and Mint Canyon floras; a fossil counterpart of *Rhus virens*, found today in Nuevo Leon, is also known in the Tehachapi flora. Axelrod suggests that the Californian element was segregated from the more generalized oak savanna of the Miocene, by the elimination of winter rainfall except on the Pacific Slope.

The distribution in California of the broad sclerophyll vegetation, that is to say, of chaparral and oak woodland, was first discussed in detail by Cooper (1922). In mapping the distribution of these associations, however, he did not distinguish between them but included in his map not only them but

what may be termed the montane chaparral, that is, species which are chaparral in type but which occur outside the main body of the community and range into the Yellow Pine forest or form an understory in it. On the basis of these combined distributions Cooper correctly concluded that California and adjacent Lower California are the present center of the broad sclerophylls, that is, of the present-day Californian segregates of Axelrod's Miocene savanna. His map shows two secondary centers, one along the coast from the region of San Francisco Bay to Monterey Bay, the other from Santa Barbara eastward to the San Bernardino Mountains.

That Cooper's conclusions are generally correct for the rather heterogeneous group which he mapped, has been adequately substantiated. However, if the present ecological segregates be considered separately, as seems desirable, the center of concentration of the chaparral is found to be somewhat different from that of the broad sclerophyll vegetation as a whole and to lie in the Diegan area.

Unlike the chaparral, the past history of the coastal sage can only be inferred from facts of present distribution and, to some extent, of floristic relationship. There are no fossil records which can be employed as a guide. The trend of aridity in the Pacific Southwest since the Eocene, which has been established by Chaney and others in numerous papers, the history of the North Mexican vegetation, which is being so admirably adduced by Axelrod, the present facts of distribution and relationship of the chaparral and coastal sage as suggested above, all these suggest an historical development for the latter which is closely parallel to that of the former.

Because of the presence of *Artemisia californica* throughout the area of the coastal sage and the habitual resemblance of the community during the growing season to the Great Basin sagebrush, it has been classed as a coastal expression of that community, as, for example, by Weaver and Clements (1929). It seems more probable to us, however, that the facts presented above and in the accompanying maps, suggest rather its derivation from the North Mexican vegetation and that *Artemisia californica* may represent an entrant absorbed from the sagebrush association, members of which have been found associated with the Tertiary woodland community, according to Axelrod (1940b).

That the development of both chaparral and coastal sage has been parallel is further suggested by the similar distribution in California of a number of species pairs which are found in both associations. The distribution of these pairs is shown in Map 8.

Mapping

In the course of the present analysis, the same chaparral species have been considered as those treated by Cooper, insofar as they represent components of the chaparral proper, save where later monographic works have led to different views of specific limits and content. The ranges of these species have been obtained directly from herbaria of Stanford University, the California

Academy of Sciences, Rancho Santa Ana Botanic Garden, Pomona College, and the University of California. The authors are much indebted to the curators of these herbaria for their consideration and take this opportunity to express their appreciation. These herbarium studies have been augmented by field observation for a period of years over the whole of the area involved, except the foothills of the Sierra San Pedro Martir and a part of the Coastal Islands.

In mapping distributions, either species or subspecies, that is, well defined geographical entities, have been employed. In the case of complex species such as *Rhamnus crocea*, for example, each geographic entity has been treated as a distributional unit. The maps are meant to indicate only the approximate limits in outline of each unit; to present their detailed distributions, even if possible from the data available, would render the essential point of this paper obscure. The distributional limits of each unit are made more explicit by the text. By mapping the limits only, without inclusion of political or topographic features, it has been possible to indicate on a few maps the essential fact of distribution of these communities, namely, that both are centered in and radiate from the Diegan Area, that is to say, San Diego County and adjacent Northern Baja California, and on the islands. The actual distribution of any single species is not pertinent to the present objective as far as the maps are concerned, but may be gained in outline by reference to the text.

Distribution

DISTRIBUTION OF CHAPARRAL

The chaparral is characterized by three elements. First, a group of wide-spread species which range from Southern Oregon to Baja California, most of them to the Sierra San Pedro Martir and one to Cedros Island (Map 1). Three of these are also found in central Arizona, leaving the Colorado desert. The actual range of the chaparral as a community is not coterminous with these limits but is more restricted. Second (Map 2), a group of species which are centered in San Diego County and Northern Lower California, referred to here as the Diegan area and which comprise with the first group, the principal and characteristic species of the community. Third, a group of species which, as pointed out by Cooper, are centered in the Monterey region, but which may also occur in the foothills of the Sierra Nevada (Map 3). The distribution of each of these elements will be considered in turn.

MAP 1.—The most widespread and characteristic species of chaparral. It will be observed that seven are found in the foothills of the Sierra Nevada. Nevertheless, the greatest concentration is in the Coast Ranges from Humboldt County southward. *Photinia* (1), *Adenostoma* (1), *Prunus* (1), *Rhus* (1), *Rhamnus* (8), *Ceanothus* (1), *Arctostaphylos* (2), *Quercus* (1), *Cercocarpus* (1).

Photinia arbutifolia—Humboldt County near Carlotta, and Shasta County, south in the coast ranges to San Diego; Sierra Nevada foothills from Butte County to Mariposa County. In Baja California on Cedros Island and apparently also in the Cape Region:

Sierra de San Francisquito, Saucito, and Sierra de Laguna. *Heteromeles salicifolia* Abrams, is evidently an ill-defined Lower Californian segregate.

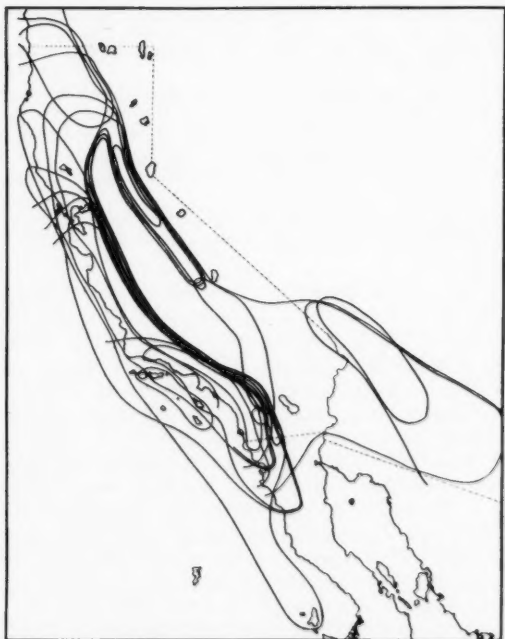
Adenostoma fasciculatum—Shasta and Trinity Counties southward in the Sierra foothills to Tulare County and southward in the Coast ranges to the Santa Ana Mountains and to the Sierra San Pedro Martii. Catalina, Santa Cruz, Santa Rosa Islands.

Prunus ilicifolia—San Mateo County, along coast to the San Rafael and Tehachapi Mts. to San Bernardino and San Jacinto Mts., to central San Diego County and in Baja California at Ojos Negros and north of Ensenada.

Rhus ovata—Santa Ynes Mts. to the Santa Ana Mts., to the San Bernardino, San Jacinto, Santa Rosa, Yaguna Mts. and the Sierra Juarez to San Pedro Martir in Lower California, westward to Alpine, San Diego County. West Central Arizona in Gila, Maricopa, Yavapai and Mohave Counties.

Rhamnus crocea subsp. *typica*—Lake County along the coast to Rio San Ysidro in Baja California.

Rhamnus crocea subsp. *ilicifolia*—Siskiyou and Shasta Counties southward in the coastal mountains and Sierra Nevada foothills to the Sierra Juarez. If in coastal Baja California, not typical and rare. In Arizona in Maricopa, Mohave, Yavapai, Coconino, Pinal, Pima, Gila, Graham and Cochise Counties.



Map 1. Distribution of fifteen widespread and characteristic species or subspecies of the chaparral.

Ceanothus cuneatus—Southwestern Oregon along coastal mountains to San Luis Obispo County, California, to the Liebre, San Gabriel, San Bernardino, Santa Rosa and Laguna Mountains to Jacumba and along the Sierra Nevada foothills from Siskiyou to Kern Counties.

Rhamnus californica subsp. *typica*—Siskiyou County southward in the coastal mountains to the Santa Ana Mts.

Rhamnus californica subsp. *occidentalis*—Southwestern Oregon southward in California through Del Norte, Humboldt, Trinity, Siskiyou and Shasta Counties.

Rhamnus californica subsp. *crassifolia*—Inner north Coast Ranges in Trinity County, California and southward to Napa and Lake Counties.

Rhamnus californica subsp. *tomentella*—Trinity and Shasta Counties, California, south in the Sierra Nevada foothills to Mariposa County; southward in the inner North Coast Ranges and in the Coast Ranges to Los Angeles County, Sierra Juarez and Sierra San Pedro Martir in Baja California.

Rhamnus californica subsp. *cuspidata*—East and west slopes of the Sierra Nevada from Mono and Madera Counties southward through the Tehachapi Mountains to the San Gabriel, San Bernardino, San Jacinto and Santa Ana Mountains.

Rhamnus californica subsp. *ursina*—Providence Mountains, California, to southeastern Arizona.

Arctostaphylos pungens—Santa Margarita in San Luis Obispo County, California, and the Santa Ynez Mountains, through the San Rafael, Liebre, San Gabriel, San Bernardino, San Jacinto, Cuyamaca and Laguna Mountains to Jacumba, and the Sierra Juarez in Baja California.

Arctostaphylos tomentosa—Santa Cruz and Monterey Counties to the Santa Ynez, San Gabriel, San Bernardino, and San Jacinto Mts. to the Cuyamaca Mountains and San Diego and the Sierra Juarez in Baja California. Santa Cruz and Catalina Islands.

Quercus dumosa—Because of the wide range and unsatisfactory taxonomic status of this complex, no attempt is made to give a detailed distribution. It ranges over most of the climax area.

Cercocarpus betuloides—Because of the wide range and unsatisfactory taxonomic status of this complex, no attempt is made to give a detailed distribution. It ranges over most of the climax area.

MAP 2.—Thirty-seven species or subspecies: *Ceanothus* (13), *Arctostaphylos* (7), *Adenostoma* (2), *Cercocarpus* (3), *Rhus* (2), *Prunus* (1), *Penstemon* (2), *Ribes* (2), *Pickeringia* (2), *Photinia* (1), *Rhamnus* (2).

It will be observed that while two species range as far as San Francisco Bay, one of these ranging also into the southern Sierra Nevada, most occur south of Santa Barbara. Four range to the Sierra Calmalli, Cedros Island and Guadalupe Island in Lower California. A majority, however, find their southern terminus along the coast at the Rio San Antonio in Lower California, and in the interior on the lower slopes of the Sierra San Pedro Martir. All are members of the Diegan flora of western San Diego County and adjacent Lower California save four which do not reach so far south and seven which are insular endemics. This element together with the first, a total of fifty-four species or subspecies, forms the main mass of the chaparral climax. It must be remembered, however, that the limits of the climax community are generally more restricted than the limits of many of these species, inasmuch as they range into other communities.

Ceanothus verrucosus—Encinitas, California, southward along the coast to Rio San Antonio and the Sierra San Pedro Martir in Baja California.

Ceanothus Palmeri—Santa Ana, San Jacinto, Cuyamaca, Palomar and Laguna Mts. Santo Tomas in Baja California.

Ceanothus tomentosus var. *olivaceus*—Santa Ana, San Jacinto and San Bernardino Mts. southward to the Sierra Juarez, and the Sierra San Pedro Martir in Baja California, and in western San Diego County to Rio San Antonio in Lower California. This subspecies probably merits specific recognition.

Ceanothus spinosus—San Luis Obispo County, along the Coast to the Santa Monica and Santa Ana Mts.

Ceanothus arboreus—Santa Catalina, Santa Cruz, and Santa Rosa Islands.

Ceanothus cyaneus—Region of Lakeside, San Diego County.

Ceanothus crassifolius—Carpinteria and the Santa Ynez Mts., southward in the Santa Monica, San Gabriel, San Bernardino, San Jacinto and Santa Ana Mts. to Lakeside and Ramona, San Diego County, to Ensenada in Baja California; Santa Cruz Island.

Ceanothus austromontanus—Cuyamaca Mountains, San Diego County.

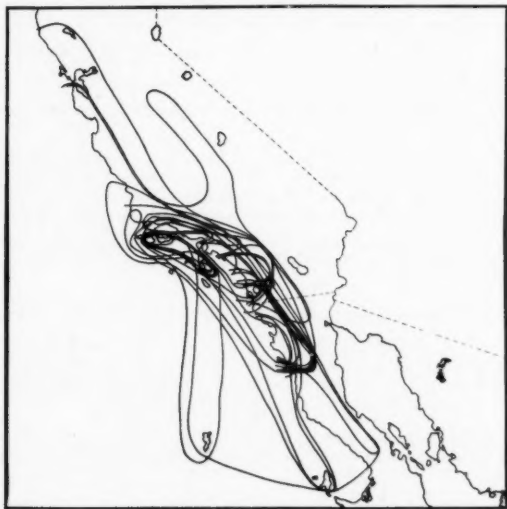
Ceanothus Orcuttii—Santa Ana and San Jacinto Mts., southward to the Cuyamaca Mts., Ramona and San Diego.

Ceanothus megacarpus—Gaviota Pass to the Santa Monica and Santa Ana Mts.

Ceanothus megacarpus var. *insularis*—Santa Catalina, Santa Cruz, and Santa Rosa Islands.

Ceanothus divaricatus—Alameda, southward along the coast to Santa Ynez, Liebre and Tehachapi Mts., northward to Nevada County in the foothills of the Sierra Nevada, and southward in the San Gabriel, San Bernardino, San Jacinto, Cuyamaca, Laguna and Santa Ana Mts., to the Sierra Juarez and San Pedro Martir in Baja California.

Ceanothus oliganthus—Santa Ynez, Santa Monica, San Gabriel, San Bernardino, Palomar and Cuyamaca Mts., to Barrett, San Diego County.



Map 2. Distribution of 27 species or subspecies of the chaparral climax.

Photinia arbutifolia var. *macrocarpa*—San Clemente, and Catalina Islands.

Arctostaphylos pechoensis—San Luis Obispo and Santa Barbara Counties along the coast, Santa Catalina and Santa Cruz Islands.

Arctostaphylos insularis—Santa Catalina, Santa Cruz and Santa Rosa Islands.

Arctostaphylos glauca—Monterey, San Benito Counties and Mt. Diablo, southward through the Santa Ynez, San Rafael, Liebre, San Gabriel, San Bernardino, Little San Bernardino, San Jacinto and Cuyamaca Mts., to Fallbrook and Jacumba. Sierra San Pedro Martir in Baja California.

Arctostaphylos subcordata—Santa Cruz, Santa Catalina, and Santa Rosa Islands, Monterey, and Santa Lucia Mts.

Arctostaphylos bicolor—Sunland, Los Angeles County, Encinitas, Fallbrook, and Pala, southward in western San Diego County to the Rio San Antonio in Baja California.

Arctostaphylos oppositifolia—Northernmost Baja California, southward along the coast to Rio San Antonio, and the Sierra San Pedro Martir.

Arctostaphylos diversifolia—Santa Monica Mts. to San Diego. Santa Catalina, Santa Cruz, and Santa Rosa Islands.

Rhamnus crocea subsp. *pilosa*—Santa Rosa, Santa Cruz, Santa Catalina, San Clemente, and Guadalupe Islands.

Rhamnus crocea subsp. *insula*—In Lower California from Santo Tomas to the Sierra San Pedro Martir.

Adenostoma fasciculatum var. *oblusifolium*—Torrey Pines Park to Jacumba, and the Sierra Juarez, and the Sierra San Pedro Martir and along the coast to Rio San Antonio.

Adenostoma sparsifolium—Cuyama Valley, Santa Barbara County, southward through the Santa Monica, San Jacinto, Palomar and Laguna Mts. to the Sierra Juarez, and the Sierra San Pedro Martir in Baja California.

Cercocarpus alnifolius—Santa Cruz, Santa Rosa, and Santa Catalina Islands.

Cercocarpus Traskiae—Santa Cruz, and Santa Catalina Islands.

Cercocarpus minutiflorus—Lake Hodges and Poway to Alpine and San Diego, and southward to Rio San Antonio in Baja California.

Rhus laurina—Santa Barbara County, and Mt. Pinos, southward through the Santa Monica and San Gabriel mountains, to western San Diego County and to the Sierra San Pedro Martir, and the Sierra Calmalli in Baja California, and along the coast to Rosario. Santa Catalina, San Clemente, Cedros, and Guadalupe Islands.

Rhus integrifolia—Santa Barbara, to the San Bernardino Mts., and southward along the coast to Rosario in Baja California. Santa Cruz, Santa Rosa, San Miguel, Santa Catalina, San Clemente, and Cedros Islands.

Prunus Lyonii—Santa Cruz, Santa Rosa, Santa Catalina, and San Clemente Islands.

Penstemon cordifolius—San Luis Obispo County, to the San Rafael Mts., and Mt. Pinos, and southward to the Santa Monica and San Gabriel Mts., and Santa Ana and Palomar Mts., to Tecate, and the Rio San Antonio in Baja California. Santa Catalina, San Clemente, Santa Cruz, and Santa Rosa Islands.

Penstemon antirrhinoides—San Bernardino, San Jacinto, and Santa Ana Mts., southward to Tecate, the Rio San Antonio, and the Sierra San Pedro Martir in Baja California.

Ribes speciosum—Along the coast from Santa Clara County to the Rio San Antonio in Baja California.

Ribes viburnifolium—Ensenada to Rio San Antonio in Baja California; Santa Catalina, and Cedros Islands.

Pickeringia montana—Lake County, southward along the coast ranges to the Santa Monica, and San Gabriel Mts.

Pickeringia montana var. *tomentosa*—San Bernardino Mts. (City Creek), Jamul, Dulzura, San Miguel Mt. and Otay Mt., San Diego County.

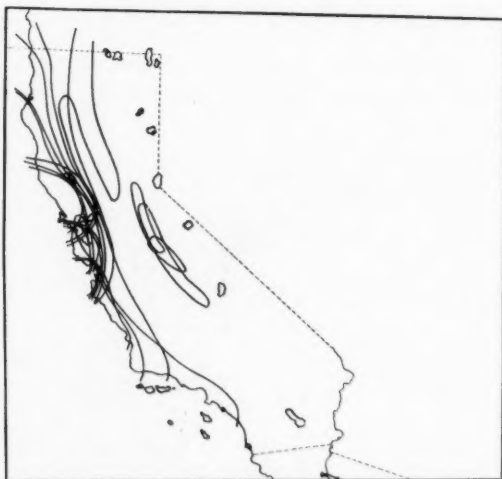
MAP 3.—Eighteen species or subspecies: *Ceanothus* (9), *Arctostaphylos* (6), *Photinia* (1), *Garrya* (1), and *Eriodictyon* (1) are centered in the central California area. Of these, two occur in the Sierra Nevada foothills as well as in the coast ranges and one occurs only in the Sierra Nevada. One species (*C. papillosus*) is found not only in Monterey region but also in the Santa Ana Mountains. Other than this, all range northward from Santa Barbara and none are insular. Not all of these species are as typically xeric, either in structure or requirements, as the species of the first and second elements.

Ceanothus dentatus—Outer Coast Ranges from Santa Cruz Mts. to Santa Barbara.

Ceanothus foliosus—Western Mendocino County and Mt. Hanna, Lake County, to Hoods Peak Range, Sonoma County, Mt. Tamalpais, Marin County, and the Santa Cruz Mts.

Ceanothus incanus—Humboldt County to the Santa Cruz Mts.

Ceanothus papillosus—Santa Cruz Mts. to the Santa Lucia Mts. and San Luis Obispo and in the Santa Ana Mountains.



Map 3. Distribution of eighteen species or subspecies of chaparral which are centered in Central California.

Ceanothus Parryi—Napa to western Humboldt and Mendocino Counties.

Ceanothus rigidus—Mt. Tamalpais to Monterey.

Ceanothus soredialis—Monterey to Mendocino County and western Solano County.

Ceanothus thyrsiflorus—Del Norte County to Monterey.

Ceanothus tomentosus—Placer County to Mariposa County in the Sierra Nevada foothills.

Photinia arbutifolia var. *cerina*—Templeton to N. Monterey County.

Garrya elliptica—Western Oregon to Santa Lucia Mts., California.

Eriodictyon californicum—Siskiyou County southward in the coast ranges to Monterey.

Arctostaphylos Andersonii—Oakland Hills to the Santa Cruz Mts.

Arctostaphylos Hookeri—Coastal Ranges from San Francisco to San Luis Obispo County.

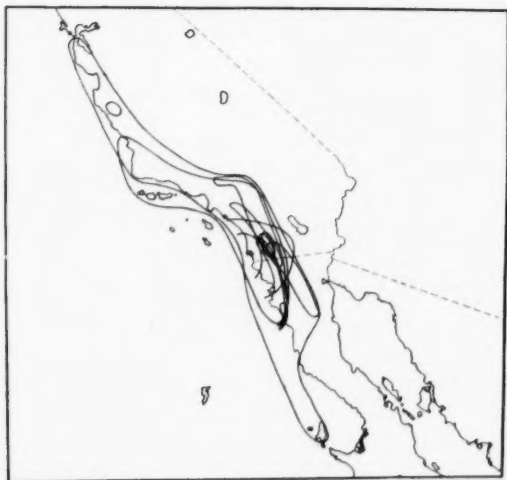
Arctostaphylos mariposa—In the higher foothills of the Sierra Nevada from Tuolumne County to Fresno County.

Arctostaphylos pumila—Region of Monterey.

Arctostaphylos stanfordiana—Mendocino and Lake Counties to the Napa Range and Mt. Hamilton.

Arctostaphylos vestita—Region of Monterey.

MAP 4.—Within the Diegan climax chaparral a number of species regularly occur which are not themselves chaparral in type. They do not ordinarily occur with the coastal sage. The ranges of twelve are given below; more might be added.



Map 4. Distribution of twelve associates of the Diegan chaparral not themselves chaparral in type.

Lonicera subspicata subsp. *typica*—Region of Santa Barbara.

Lonicera subspicata subsp. *denudata*—Fallbrook to San Diego, and the Sierra San Pedro Martir; Cedros Island.

Lonicera subspicata subsp. *Johnstonii*—Santa Clara southward to the Santa Monica, San Gabriel, Santa Ana, San Bernardino, San Jacinto, Laguna Mts., and in Baja California in the Sierra Juarez, and the Sierra San Pedro Martir.

Salvia Clevelandii—Santa Margarita, San Diego County, to the Rio San Antonio in Baja California.

Lathyrus splendens—Escondido to Jacumba, and the Sierra Juarez in Baja California.

Silene laciniata—San Luis Obispo and Santa Barbara Counties, to the Santa Monica, and San Gabriel Mts., to Palomar, and Julian, and the Laguna Mts., to San Diego, and Rio San Antonio in Baja California. Santa Cruz, and Santa Rosa Islands.

Satureja Chandleri—Murieta, Orange County, and San Miguel Mt., San Diego County.

Satureja Ganderi—Rio San Antonio, Baja California.

Trichostema Parishii—San Gabriel, San Bernardino, San Jacinto, Cuyamaca, and Laguna Mountains to the Sierra Juarez, and to the Rio San Antonio, and the Sierra San Pedro Martir in Baja California.

Chamaebatia australis—South central San Diego County, to Rio San Antonio in Baja California.

Monardella macrantha—Santa Lucia Mts., San Bernardino Mts., Descanso, San Pedro Martir.

Yucca Whipplei subsp. *typica*—Santa Ana, San Jacinto, Santa Rosa, and Laguna Mts. to the coast of Baja California so far as the Rio San Ysidro.

DISTRIBUTION OF THE COASTAL SAGE

The geographic limits of the coastal sage are approximately those of the chaparral species which are centered in the Diegan area. The community is found at lower elevations and in drier sites.

MAP 5.—The following are dominant and for the most part, widespread species: *Eriodictyon* (2), *Salvia* (4), *Viguera* (1), *Encelia* (1), *Lotus* (5), *Artemisia* (1), *Franseria* (1), *Eriogonum* (2).

Eriodictyon sessilifolium—La Grulla canyon, and Guadalupe Valley to Rosario, Baja California.

Eriodictyon crassifolium—San Rafael Mts., and Mt. Pinos region, southward to San Bernardino, San Jacinto, Santa Ana Mts., and San Diego.

Salvia mellifera—Santa Cruz Mts., and Mt. Diablo, southward in the coast ranges to the San Bernardino Mts., and San Diego. Santa Cruz, San Clemente, and Santa Catalina Islands.

Salvia Munzii—Otay Mt., San Diego County, southward along the coast to Rosario, Baja California.

Salvia apiana—Santa Barbara to the San Gabriel, San Bernardino, San Jacinto, Santa Ana, Santa Rosa, and Laguna Mts., to the Sierra San Pedro Martir. Along the coast nearly to Punta Prieta in Baja California.

Salvia Brandegei—Santa Rosa Island.

Viguera laciniata—San Onofre to San Diego, and southward in Baja California to the Sierra Calmalli.

Encelia californica—Santa Barbara, southward along the coast to the Sierra Calmalli in Lower California. Santa Cruz, Santa Catalina, San Benito, and San Clemente Islands.

Lotus scoparius (typical)—Mendocino and Sonoma Counties southward to the Santa Monica, San Gabriel, Tehachapi, and San Bernardino Mts., to Socorro in Baja California.

Lotus scoparius var. *brevialatus*—San Bernardino, Santa Rosa, Little San Bernardino Mts., to the Laguna Mts., and to Rio San Antonio in Baja California.

Lotus scoparius var. *Veatchii*—Cedros Island, San Miguel Island.

Lotus scoparius var. *Traskiae*—Santa Catalina Island.

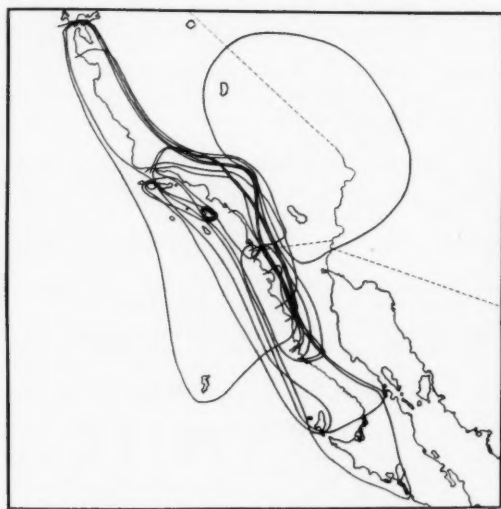
Lotus scoparius var. *dendroideus*—Santa Catalina, Santa Cruz, and Santa Rosa Islands.

Artemisia californica—San Mateo, Contra Costa, and Alameda Counties, southward along the coast to the Santa Ana and San Bernardino Mts., and to San Quintin in Baja California. Santa Catalina, San Clemente, Santa Cruz, Santa Rosa, Santa Barbara, Anacapa, Guadalupe, and Cedros Islands.

Franseria chenopodifolia—San Ysidro, southward along the coast to Calmalli, and Magdalena Island; Cedros Island.

Eriogonum fasciculatum—San Benito County and Monterey Bay, southward along the coast to the Sierra San Pedro Martir in Baja California, and from Bakersfield and Lone Pine southward to the San Bernardino Mts., along the western margin of the Colorado Desert into Baja California, and eastward into southern Nevada, southwestern Utah and to central Arizona.

Eriogonum fastigiatum—Cabo Colnett to Rosario, Baja California.



Map 5. Distribution of the Coastal Sage. Typical widespread species and subspecies.

MAP 6.—The following are species more or less similar in habit to the principal components of the coastal sage, but not abundant and never dominant: *Romneya* (1), *Astragalus* (2), *Ambrosia* (2), *Iva* (1), *Haplopappus* (3), *Rosa* (1), *Lotus* (1), *Chlorogalum* (1), *Atriplex* (1).

Romneya Coulteri—Santa Barbara County southward to the Hamilton Ranch, and the Sierra San Pedro Martir in Baja California.

Astragalus leucopsis—Morro, San Luis Obispo County and the Santa Monica Mts., southward along the coast nearly to Rosario, Lower California. Santa Catalina, Santa Cruz, and Santa Rosa Islands.

Astragalus oocarpus—Ramona, Witch Creek, Descanso and Julian in San Diego County.

Ambrosia pumila—San Diego to Ensenada.

Ambrosia psilostachya—Los Angeles to the San Bernardino Mts., and southward to western San Diego County.

Iva Haynsiana—San Diego, Lake Hodges, Jamul, and San Miguel Mt. to Socorro, Baja California; Cedros Island.

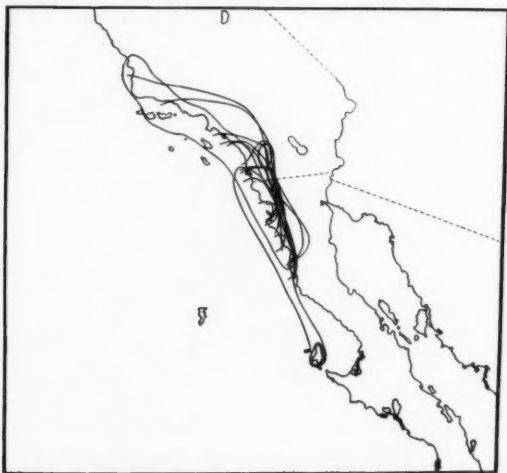
Haplopappus venetus oxyphyllus—Santa Maria and Santa Barbara, southward to the San Pedro Martir in Baja California.

Haplopappus junceus—San Diego to Alpine, and Descanso, and southward to Tecate.

Haplopappus berberidis—Coronados Islands and the mainland, southward to the Sierra San Pedro Martir, Baja California.

Rosa minutifolia—Ensenada to Rosario, Baja California.

Louisa Nuttallianus (*Hosackia prostratus*)—San Diego, southward to San Quintin, Baja, California; Cedros Island.



Map 6. Distribution of Coastal Sage. Associated species which occur in or enter the Diegan area.

Chlorogalum parviflorum—From Lake Elsinore (Menifee), southward to the Cuyamaca Mts., and to San Diego, and Tijuana, and Valle Redondo in Baja California.

Atriplex julacea—Todos Santos Island, along the coast to San Bartolome Bay (? and south and east).

MAP 7.—Woody associates of the coastal sage in the Diegan area.

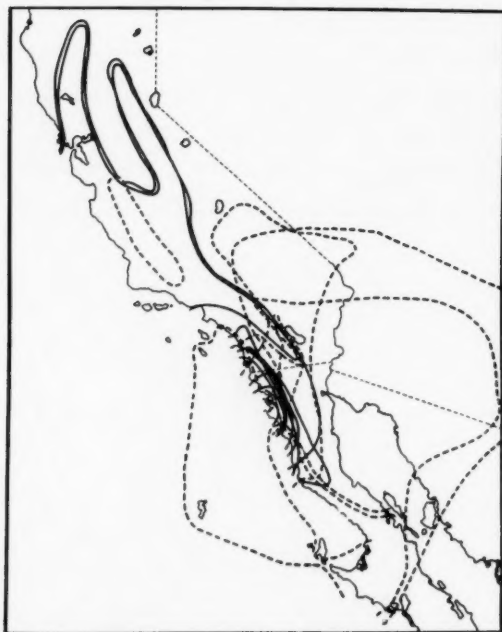
Tetradlea dioica—Fallbrook and Temecula, San Diego County, to Santo Tomas, and El Refugio, Baja California.

Fraxinus trifoliata—Carrizo Creek to Ensenada, and southward to the Sierra San Pedro Martir, Baja California.

Ptelea aptera—Punta Banda near Ensenada, to Cuesta Sacaton, Baja California. *Aesculus Parryi*—Guadalupe to Ensenada, and southward to Rosario, Baja California.

Adolphia californica—San Diego, southward to Rosario, and Jaraguay, Baja California.

Cneoridium dumosum—Encinitas, San Diego County, southward to the Sierra San Pedro Martir, Baja California.



Map 7. Distribution of woody associates of the Coastal Sage Climax in the Diegan area. The solid lines indicate the associates which are shared in part by the adjacent communities, or are similar to species in them; the broken lines indicate entrants from the *Larrea-Franseria* climax.

Dendromecon rigida—Shasta County, southward to San Diego, and Jacumba, and the Sierra San Pedro Martir, Baja California.

Fremontia californica—From Redding in Tehama County, southward along the foothills of the Sierra Nevada to the Tehachapi Mountains and along the coast ranges to the San Gabriel, San Bernardino, and Laguna Mountains.

Fremontia mexicana—Jamul Valley in San Diego County to the Rio San Antonio, Baja California.

Rhus integrifolia and *R. ovata*, although typically chaparral, are frequent associates; the latter ranges into the *Larrea-Franseria* climax.

MAP 7.—Entrants from the *Larrea-Franseria* climax.

Simmondsia californica—Bonsall to Aguanga, San Diego County, to the Rio San Antonio, Baja California, eastward through Colorado Desert.

Encelia farinosa—Riverside, Elsinore, and Ensenada, Baja California, eastward and southward through the Colorado Desert.

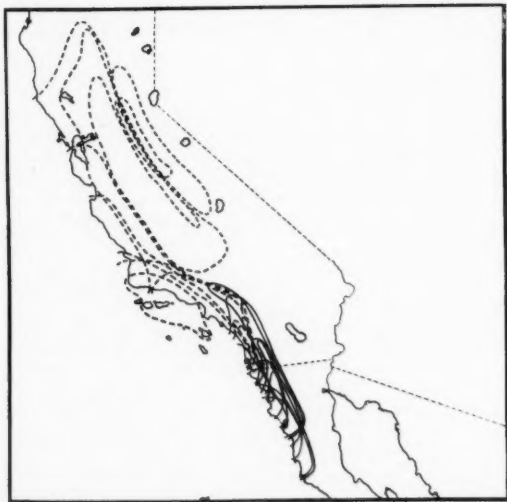
Ephedra californica—San Diego to Jacumba, and southward to San Quintin, Baja California, eastward through Colorado Desert.

Euphorbia misera—San Diego to Sierra Calmalli, and southward, Baja California. San Clemente, San Marcos, Cedros, Guadalupe Islands.

Prunus eriogyna—Santa Rosa Mts. to Jacumba, and westward to Ensenada and Santo Tomas.

Harfordia macroptera—Cabo Colnett to Sierra Calmalli, and southward in Baja California; Cedros Island.

MAP 8.—Pairs of species which occur either in the coastal sage or chaparral, one member of the pair having a southern, the other a northern distribution. Other similar pairs, or pairs of clearly marked subspecies might be added.



Map 8. Species of the Diegan area which have vicarious species in central California (broken lines).

Fraxinus dipetala
Fraxinus trifoliata
Chamaebatia foliolosa
Chamaebatia australis
Eriodictyon crassifolium
Eriodictyon sessilifolium
Salvia mellifera
Salvia Munzii
Aesculus Parryi
Aesculus californica
Satureja Chandleri

Satureja Ganderi
Trichostema Parishii
Trichostema lanatum
Ceanothus tomentosus
Ceanothus tomentosus var. *olivaceus*
 (apparently distinct)
Ceanothus verrucosus
Ceanothus megacarpus
Ceanothus Palmeri
Ceanothus spinosus

Conclusions

The chaparral and coastal sage associations of California have their present centers of distribution in the Diegan area, that is, in San Diego County, and in adjacent Baja California.

It seems probable that both communities have had a similar historical development and that both are derivatives of the Miocene vegetation which entered the Southwestern United States from the North Mexican Plateau.

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Great Basin Plants - VII. Cruciferae

Bassett Maguire

During the study of recently collected material of the *Cruciferae* and routine herbarium work a number of interesting records have appeared, and problems been uncovered which necessitate comment. In the course of the review of materials in certain genera it has been found necessary to obtain loan of specimens from a number of institutions. Acknowledgment and expression of appreciation is made to the curators of the New York Botanical Garden (NY), Rocky Mountain Herbarium (RM), the University of Utah (UU), Brigham Young University (BY), and to Professor A. O. Garrett (Garrett).

DESCURAINIA PINNATA (Walt.) Britt. ssp. GLABRA (Woot. & Standl.) Detl., dry sandy soil, assoc. with *Coleogyne*, Silver Reef, Washington County, Utah, April 11, 1937, Maguire, no. 20455. The subspecies is commonly represented in the upper extremities of the Mohave Desert, reaching into Washington County, Utah.

LESQUERELLA

In the Great Basin and Intermountain Region there are at least six more or less distinct populations centering about *Lesquerella Kingii*. Four of these have previously been recognized by students of the group. Two are proposed as new in this paper.

That the members of this complex are closely interrelated and difficult of interpretation has been pointed out by Payson.¹ Because little new light can be shed on the problem, I quote at length from his interesting discussion.

L. Kingii was the first of a number of forms to be described from the region of the Great Basin that are here being treated as species. These are *L. Wardii*, *L. prostrata*, *L. utahensis*, and *L. latifolia*. The differences between them are slight and within their specific limits they show considerable variation. There is evidently here a remarkable plexus of evolution due perhaps to some germinal plasticity or perhaps to the topographical character of the country that isolates races on every detached mountain range. However the presence of such an assemblage of minute forms may be explained, the result remains difficult of treatment by the taxonomist. Perhaps they were best regarded as varieties under one great species, but in the present case this might easily result in a polyphyletic group and so emphasize an unnatural relationship.

It seems to me, likewise, because of general prevalence of intermediacy and confluence of form, that the entities discussed by Payson with the probable exception of *L. latifolia* might be treated as geographic subspecific populations of a single species. Or perhaps a more acceptable disposition would be to

¹ Payson, E. B. A Monograph of the Genus *Lesquerella*. Ann. Mo. Bot. 8:216. 1921.

consider the entities with rounded pods as a single species, with *L. Kingii* representing the western race, and *L. utahensis* the eastern representative of the species. The population with more elongate and somewhat acutish pods is represented by *L. Wardii* from south-central Utah, and by *L. prostrata* to the north. It is felt, however, that any such formal alignment should best await a more competent and thorough survey and revision of the entire genus.

The following key and brief discussion may help to clarify the relationship and distribution of the species-group *Kingii*.

- A. Mature pods more or less elongate, acutish at the apex.
 - B. Pods (5) 6-8 mm long; leaf blades frequently subhastate or toothed; plant of southeastern Idaho, southwestern Wyoming, and probably the Uinta Mts of northeastern Utah1. *Lesquerella prostrata*.
 - B. Pods (4) 6-8 mm long (10 mm long acc. to Payson); leaf blades entire, seldom subhastate, plants of south central Utah2. *Lesquerella Wardii*.
- A. Mature pods more or less spherical, rounded or obtuse at the apex.
 - B. Caudex not multicapital, little or not at all branched.
 - C. Pods 4-6 mm long; branches frequently ascending; plants of Nevada, and southeastern adjacent California3. *Lesquerella Kingii*.
 - C. Pods 4-6 mm long; branches prostrate; plants of the Wasatch Range and high Western Plateau of Utah4. *Lesquerella utahensis*.
 - B. Caudex multicapital, the branches slender, born on a slender root; plants of the Bear River Range, Utah and adjacent Idaho, and southwestern Wyoming.....5. *Lesquerella multiceps*.
- A. Mature pods emarginate; plants of central Utah6. *Lesquerella hemiphsaria*.

1. *LESQUERELLA PROSTRATA* A. Nels. Bull. Torr. Club. 26:124. 1899.

By virtue of the elongate and acutish pods plants going under this name seem to be most closely related to *L. Wardii* of similar character, and perhaps represents at best, merely a northern representative of that species.

2. *LESQUERELLA WARDII* S. Wats. in Gray, Syn. Fl. N. Am. 1:118. 1895.

Very close to the preceding, differing only slightly in the general leaf form, and the frequently smaller pods. The leaves in *L. prostrata* are frequently subhastate or even somewhat toothed, whereas in the present entity, the leaves are mostly entire.

3. *LESQUERELLA KINGSII* S. Wats. Proc. Am. Acad. 23:251. 1888.

Together with the next, forming a population with subspherical pods, but primarily differing from it in a more ascending habit, fewer branches, and less dense racemes.

4. *LESQUERELLA UTAHENSIS* Rydb. Bull. Torr. Club 30:252. 1903.

Of the *Kingii* complex, *L. utahensis*, as treated by Payson, was the most

polymorphic and ill-defined group. Field observation, and examination of considerable material including Rydberg's type (which apparently Payson did not see) demonstrates conclusively that within it there are three distinct entities involved; this immediate population containing the type, and the two following species.

The type of *L. utahensis*, American Forks Canyon, July 31, 1880, altitude 9000 feet, Utah County, Utah, *M. E. Jones*, no. 1354 (NY) consists of a series of 4 rather small specimens, with subspherical fruit, ca. 4 mm long, somewhat dense racemes, non-hastate entire leaves, and prostrate stems. These are the characteristic plants of the higher mountain regions of the Wasatch Range. Southward the population extends into the Tushar Range where it meets and tends to become confluent with *L. Wardii*. One series of specimens, rocky ridges, Dyer Mine, Uinta Mts., Utah, July 5, 1902, *L. N. Gooding*, no. 1258 (RM) seem to represent an intermediate condition between *L. utahensis* and *L. prostrata*.

5. *Lesquerella multiceps* sp. nov.

Herba perennis, multicapitalis; caulibus procumbentibus, simplicibus, foliis principalibus laminis vel elliptico-oblancoelatis, 5-10 mm latis, 1-2 cm longis, foliis racemosis, laxis; siliculis subglobosis 3-4 mm longis, stylo 4-5 mm longo; loculis 2-ovulatis; seminibus orbiculatis emarginatis ca. 2 mm. latis.

Perennial; loosely multicapital from a slender tap root; branches of the caudex slender, frequently numerous, mostly 3-5 cm long, terminating in short leafy shoots; lateral flowering branches usually 2-3 from each caudex branch. (5) 8-12 cm long, slender, prostrate or ascending, sparsely stellate-pubescent, the 2-5 leaves of the flowering stems oblanceolate, reduced; principal leaves (2) 3-5 cm long, the blade elliptic to elliptic-oblancoelate, 5-10 mm broad, 1-2 cm long, somewhat abruptly or gradually narrowed into a slender petiole $1\frac{1}{2}$ to 3 times longer than the blade; stellate-pubescent dense, particularly on the newer leaves, stellae 0.5-0.8 mm diam., rays numerous, fused for $\frac{1}{3}$ of their length or less; inflorescence racemose, elongate, remotely flowered; pedicels 5-8 mm long, spreading and strongly upwardly sigmoid-curved; petals yellow, drying pink, oblanceolate, obtuse, 7-10 mm long; sepals 4-5 mm long, oblong-linear, characteristically pink-tinged; siliques sub-sessile, globular slightly broader than long, rounded at the apex, rarely somewhat acutish; scantily pubescent, 3-4 mm long; styles 4-5 mm long, stigma expanded; ovules 2 in each loculus, suspended from near the apex; funiculi attached for $\frac{1}{2}$ their length; seed marginless, orbicular, ca. 2 mm broad.

L. multiceps as here delimited is probably most closely related to (and included by Payson within) *L. utahensis*, as is evidenced by the similar fruit. The striking multicapital habit, the elliptical leaf blades, the slender longer petioles, and the loosely flowered raceme make this one of the most distinctive species of the complex. Specimens from the Bear River Range, Cache County, Utah, cited by Payson under *L. utahensis*, are to be referred here.

TYPE: Frequent, limestone ledges and ridges, vic. Tony Grove Lake, 8300 feet, August 4, 1938, Bear River Range, Cache County, Utah, *Maguire*, no. 16030 (Ut).

SPECIMENS SEEN: IDAHO: Bloomington Lakes, Bear River Range, Bear Lake County, June 2, 1939, Ray J. Davis, no. 980 (Ut).—UTAH, Cache County: dry soil, Mt. Logan, 9000 feet, June 24, 1924, Flowers, no. 689 (UU); Logan Peak, 9700 feet, August 31, 1931, Maguire, no. 186 (Ut); dry gravelly wash, 10 miles up Smithfield Canyon, 6000 feet, Bear River Range, June 14, 1936, Maguire, no. 13681 (Ut); gravelly wash, stream side, 8 miles up Smithfield Canyon, 6000 feet, Bear River Range, Maguire, no. 13685 (Ut); stony ridges in Spruce, vic. Tony Grove Lake, 8200 feet, Bear River Range, July 3, 1936, Maguire, no. 13944 (topotype, Ut); rocky soil east exposure, summit Mt. Naomi, Bear River Range, July 20, 1936, Maguire, et al., no. 14183 (Ut); slopes of fir belt, Spring Hollow, 7500 feet, Bear River Range, May 20, 1934, Maguire, no. 20362 (Ut); among cliffs on east slope of Naomi Peak, Bear River Range, June 3, 1934, Maguire, no. 20363 (Ut); dry slopes, Mt. Logan, 7500 feet, Bear River Range, May 20, 1934, Maguire, no. 20364 (Ut); Mt. Logan ridge, 8700 feet, July 4, 1910, C. P. Smith, no. 2244 (NY, Ut, RM); Logan Peak, 10,000 feet, July 4, 1910, C. P. Smith, no. 2248 (NY, RM, Ut).—WYOMING: stony upper slopes, Sheep Mountain (Ferry Peak), Snake River Range, near Alpine, Lincoln County, July 11, 1923, B. Payson and G. M. Armstrong, no. 3466 (2RM).

6. *Lesquerella hemiphsaria* sp. nov.

Herba perennis, caespitosa; caulibus prostratis, simplicibus; foliis radicalibus laminibus ellipticis vel elliptico-rhomboideis, 8-12 mm longis, 4-8 mm latis; floribus racemosis aliquantum congestis; siliculis late obovatis, emarginatis, 3-5 mm longis, 4-7 mm latis; stylo 4-7 mm longo; loculis 4-9 ovulatis; seminibus marginatis, 2-2.5 mm longis, 1.3-1.8 mm latis.

Perennial, caudex simple, or somewhat closely branched, born on a stout tap root; terminal but not developing; branches numerous, 6-12 cm long, slender, prostrate; basal leaves frequently forming a rosette, 2-4 cm long, the blades elliptic to elliptic-rhomboid, 8-12 mm long, 4-8 mm broad, obtuse, abruptly narrowed to a slender petiole, stem leaves oblanceolate to spatulate, reduced, petiole short; inflorescence racemose, 2-6 cm long, rather densely flowered; pedicels ascending, straight to slightly sigmoid, 2-5 mm long; sepals oblance-oblong, 5-6 mm long, obtuse, frequently reddish tinged; petals yellow oblanceolate, 10-12 mm long, slightly retuse, claw somewhat dilated at the base; siliques sessile, 3-5 mm long, 4-7 mm broad, broadly obovate in outline, flattened contrary to the partition, emarginate at the apex, each cell somewhat inflated, mostly reddish, more or less densely pubescent; styles abruptly capitate, 4-7 mm long, exceeding length of pod; ovules 4-8 (mostly 6), in each cell, suspended from above the middle, funiculi attached for 1/3 of their length; seed brown, smooth, dorsally margined, 2-2.5 mm long, 1.3-1.8 mm broad.

TYPE: Frequent, limestone breaks, south side Middle Forks Park, Wasatch Plateau, 10,800 feet, August 10, 1940, Sanpete County, Utah, Maguire, no. 20053.

Payson² wrote, "*L. utahensis* is perhaps the most interesting of all the species of *Lesquerella* because of the great similarity, in some of its forms particularly, to members of the genus *Physaria*. So striking, indeed, is the similarity that one is a little perplexed at times to know to which genus a given

² Payson, E. B. A Monograph of the Genus *Lesquerella*. Ann. Mo. Bot. 8:221. 1921.

plant should be referred. And yet *utahensis* as a species is not entirely satisfactory, so close is it to other forms that give no suggestion of *Physaria*. The bridge connecting the two genera is nearly complete." It is obvious that these remarks were directed mostly to the plants here delimited as *L. hemiphsaria*. The striking emarginate condition obtains nowhere else in the genus. It is interesting further to note that plants of this clear-cut species are narrowly endemic to the upper elevations of the Wasatch Plateau, a high table-land of central Utah, exceeding 10,000 feet, some 25 miles broad and 75 miles long. Other members of the complex do not occur here.

SPECIMENS SEEN: UTAH, Sampete County: nine miles up canyon, Manti Canyon, 7000 feet, July 30, 1895, *Cottam* (UU); 13 miles up canyon, dry slopes, 7500 feet, Manti Canyon, July 30, 1895, *Cottam* (UU); abundant, clay loam soil, west slope, 10,000 feet, Alpine Forest Station, Ephraim Canyon, Manti Forest, May 21, 1934, *Basil Crane* (Ut); rocky soil, gentle west slope, creek bottom, Ephraim Canyon, Manti Forest, 7000 feet, June 13, 1936, *Basil Crane* (Ut); frequent, open stony meadows, Middle Forks Park, Skyline Drive, Wasatch Plateau, Manti Forest, 10,500 feet, August 8, 1940, *Maguire*, no. 20025 (Ut); frequent, limestone breaks, south side Middle Forks Park, 10,800 feet, August 10, 1940, *Maguire*, no. 20053 (type Ut); along Sky Line Drive, near Buck Ridge Fork, Wasatch Plateau, 10,500 feet, June 23, 1934, *Ray Olsen* (Ut). Sevier County: Skyline Drive, Manti Forest, July 12, 1934, *Ray Olsen* (Ut). Emery County: dry sandy soil, near Forks of Huntington Canyon, 8500 feet, May 10, 1935, *B. F. Harrison*, no. 8166 (2 Garrett, BY).

7. *LESQUERELLA RECTIPES* Woot. & Standl. Contr. U. S. Nat. Herb. 19:217. 1915.

In Payson's monograph the Utah range for this species is San Juan and possibly Grand Counties in southeastern Utah. More recent collections of specimens referred here demonstrate it to extend throughout the Colorado Plateau south of the Uinta Basin and westward to the higher Wasatch and Plateau ranges.

SPECIMENS SEEN: COLORADO, Montezuma County: Mesa Verde National Park, 7000 feet, June 15, 1936, *W. D. Stanton* (UU).—UTAH, Carbon County: park, 12 miles northeast of Price, June 5, 1937, *Ross Hardy* (UU); dry Juniper-Pinon slopes, 8500 feet, headwaters of Left Fork of Minnie Maude Creek, West Tavaputs Plateau, 20 miles north of Wellington, June 9, 1940, *Maguire*, no. 18511 (Ut); Emery County: sandy soil, San Raphael Swell, 20 miles southwest Green River, 5500 feet, May 15, 1931, *B. F. Harrison*, no. 5602 (BY); low shrub, arid grass association, 5 miles south San Raphael River, San Raphael Swell, 6500 feet, May 11, 1940, *B. F. Harrison*, no. 9610 (BY). San Juan County: dry canyon wall, 6000 feet, Natural Bridges, June 28, 1927, *Cottam*, no. 2445 (BY); near Cottonwood Gulch, Canyon 20 miles west of Blanding, 4500 feet, May 7, 1933, *B. F. Harrison*, no. 5900 (BY); Edwin Bridge, 6023 feet, June 10, 1936, *D. Henriques*, no. 30 (UU); Elk Ridge, June 11, 1936, *D. Henriques* (UU); White Canyon, June 11, 1936, *D. Henriques*, no. 41 (UU); White Canyon, June 11, 1936, *D. Henriques*, no. 44 (UU); Rydberg and Garrett (Garrett); western slope of La Sal Mountains, near Little Springs, July 5-6, 1911, Rydberg and Garrett, no. 8558 (Garrett); Armstrong and White Canyons, near the Natural Bridges, August 4-6, 1911, Rydberg and Garrett, no. 9448 (Garrett).

8. *LESQUERELLA ALPINA* (Nutt.) S. Wats. Proc. Am. Acad. 23:251. 1883.

Bare rocky ridge, 12 miles north Manila, Ashley National Forest, 8,400 feet, Daggett County, Utah, June 20, 1934, *Harison and Larsen*, no. 7892 (BY).

This collection constitutes a record new to Utah. It was to have been expected that the plant would be found in the state, on the north slopes of the Uinta Mts., since numerous collections are known from the vicinity in adjacent Wyoming.

THELYPODIOPSIS AUREA (Eastw.) Rydb., red sandy soil, Cottonwood Wash, 2 miles west Bluff, San Juan County, Utah, April 20, 1936, *Maguire*, no. 13519; sandy soil, about reservoir, Wayland Ranch, Cottonwood Canyon, 2 miles west Bluff, San Juan County, Utah, April 21, 1936, *Maguire*, no. 20457.

Described as *Thelypodium aurea* by Eastwood, *Zoe* 2:227. 1891, from Durango, Colorado, this rare species has since apparently been only locally known. The present collections represent a range extension some 150 miles westward, and into Utah.

THELYPODIUM AFFINE Greene, ditch bank vicinity St. George, Washington County, Utah, August 2, 1934, *B. Maguire & B. L. Richards, Jr.*, no. 20460. Previously known only from the western Mohave Desert.

THLASPI FENDLERI A. Gray.

In reviewing Utah and Intermountain *Thlaspi*, I have found myself in much the same dilemma in which Payson³ was placed during his revision of the genus. Large series of specimens showing all degrees of confluence, and considerable field observation have imposed the conclusion that the plants going under the name *T. Fendleri* and *T. glaucum* are conspecific—that they represent only ecological phases and in both the northern and southern parts of the general range, distinct geographical populations, *T. glaucum* and varieties northward and *T. Fendleri* southward. Much this same conviction was expressed by Payson (1 c.), "It seems doubtful if *T. Fendleri* can be maintained as specifically distinct from *T. glaucum* var. *typicum*."

Final disposition of this problem is perhaps best relegated to more competent students of the *Cruciferae*. More confidently, however, disposition may be made of the plants named by Rydberg and interpreted by Payson as *T. coloradense*.

They have been maintained by these two keen observers as distinct from *T. Fendleri*, delimited by a condensed mature inflorescence, and caespitose habit. Considerable recent material, however, demonstrate typical *T. Fendleri*, in older specimens, to be frequently caespitose, while many specimens of *T. coloradense* have produced little or not at all branched caudexes. Plants of the highest mountain peaks consistently are low, with short stems, and condensed inflorescence, while plants of lower elevations quite consistently develop longer stems and more elongate inflorescence. All intermediate conditions obtain.

On loose talus plants having the compact inflorescence of the alpine ecotype become loosely caespitose, developing extensive slender secondary branches,

³ Payson, E. B. The Genus *Thlaspi* in North America. Univ. Wyo. Publ. Bot. 1:145. 1926.

and somewhat coriaceous leaves. They apparently represent a distinct ecological variant.

KEY TO THE VARIETIES OF *THLASPI FENDLERI*

- A. Inflorescence in fruit, more or less elongate, not corymbiform; stems mostly 10-20 cm high; plants of subalpine or lower montane habitats 1. *Thlaspi Fendleri* var. *typicum*.
 A. Inflorescence in fruit short, dense, more or less corymbiform; stems 10 cm high or less, plants of alpine peaks and ridges.
 B. Caudex little or closely branched; leaves not coriaceous 2. *Thlaspi Fendleri* var. *coloradense*.
 B. Caudex loosely multicapital, the branches long and slender; leaves somewhat coriaceous 3. *Thlaspi Fendleri* var. *tenuipes*.

1. *Thlaspi Fendleri* A. Gray, var. *typicum* nom. nov.

Thlaspi Fendleri A. Gray (Pl. Wright.) Smithson. Contr. 5:14. 1853.

Thlaspi purpurascens Rydb. Bull. Torr. Club. 28:281. 1901, in part.

2. *Thlaspi Fendleri* A. Gray, var. *coloradense* (Rydb.) comb. nov.

Thlaspi coloradense Rydb. Bull. Torr. Club. 28:280. 1901.

Thlaspi purpurascens Rydb. Bull. Torr. Club. 28:281. 1901, in part.

SPECIMENS SEEN: UTAH, Grand County, La Sal Mts.: Gold Mt., 10,700 feet, July 11, 1934, *Maguire et al.*, no. 15785; Pilot Mt., July 11, 1933, 12,350 feet, *Maguire et al.*, no. 15786. San Juan County, La Sal Mts.: Saddle between Mt. Peal and Mt. Tukhunikwatz, 11,500 feet, July 5, 1932, *Maguire and Redd*; summit Mt. Peal, 13,089 feet, July 31, 1932, *Maguire et al.*, no. 15787. Iron County: summit Brian Head Peak, 11,315 feet, June 23, 1940, *Maguire*, no. 18985; 1/2 mile below summit Brian Head Peak, 10,800 feet, June 23, 1940, *Maguire*, no. 19001.

3. *Thlaspi Fendleri* A. Gray, var. *tenuipes* var. nov.

A. var. *coloradense*, caudicibus multicapitalibus atque foliis subcoriaciis differt.

Caudex multicapital; branches slender, extensive; leaves subcoriaceous; otherwise as in the var. *coloradense*.

TYPE: Frequent, loose talus, west slopes, Mayfield Canyon, 1/2 mile above Ranger Station, 10,928 feet, August 8, 1940, Sanpete County, Utah, *Maguire*, no. 19998.

This is an ecological variant probably derived from the var. *coloradense*, occurring in loose and mostly calcareous talus at high altitudes in alpine habitats, or those by virtue of special conditions simulating alpine habitats.

SPECIMENS SEEN: UTAH, Piute County: Delano Peak, 11,800 feet, July 20, 1940, *Maguire*, no. 19723 (Ut). Beaver County: Tushar (Belknap) Peak, 11,700 feet, July 22, 1940, *Maguire*, no. 19777 (Ut). Sanpete County: loose talus, Mayfield Canyon, 10,928 feet, August 8, 1940, *Maguire*, no. 19998 (type, Ut).

INTERMOUNTAIN HERBARIUM,
 UTAH STATE AGRICULTURAL COLLEGE,
 LOGAN, UTAH.

Notes on the American Flora, Chiefly Mexican

Cornelius H. Muller

Collections of plants made by the author in northern Mexico in 1939 and by Dr. Ivan M. Johnston with the author in 1940 contain several novelties and other noteworthy species, some of which are here treated. Various items from other sources which have from time to time come to the author's attention are also included. The bulk of the material here presented concerns the genus *Quercus*. The herbaria in which specimens are deposited are designated as follows:

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| (AA)—Arnold Arboretum, Harvard University. | (Ill)—University of Illinois, Urbana. |
| (ANS)—Academy of Natural Sciences of Philadelphia. | (MBG)—Missouri Botanical Garden, St. Louis. |
| (F)—Field Museum of Natural History, Chicago. | (Mu)—Author's collection. |
| (G)—Gray Herbarium, Harvard University. | (T)—University of Texas, Austin. |
| | (US)—U. S. National Museum, Washington. |
| | (USNA)—U. S. National Arboretum, Washington. |

FAGACEAE

Quercus albaefolia sp. nov.

Arbor parva, ramuli 2-3 mm. crassi, dense vel sparse stellato-pilosi, tarde glabrati, folia decidua, 5-15 cm. longa, 3-8 cm. lata, anguste ovata vel oblonga, apice obtusa, basi cuneata vel rotunda inciso-lobata, lobi utrinque 5-9 rotundi vel rare acuti, utrinque glabra vel sparse minute stellato-puberulenta, venis utrinque 5-9, petioli 12-22 mm. longi, dense villosi, fructus annuus, solitarius vel binus brevipedunculatus, cupula 15-17 mm. lata, 10 mm. alta, glans 15 mm. longa, 12 mm. lata, $\frac{1}{2}$ inclusa.

Small tree to 6 m. in height, the trunk 2.5 dm. in diameter with scaly or furrowed gray bark. Twigs 2 to 3 mm. thick, broadly and shallowly sulcate, tan or grayish-brown, densely tawny-pilose or sparsely stellate-pubescent, becoming glabrous the second year and light gray with a few large but inconspicuous lenticles. Buds 3 to 4 mm. long, 1.5 to 2 mm. broad, oblong or ovoid, shiny light brown, the scales centrally opaque with broad reddish hyaline margins, ciliate and otherwise glabrous. Stipules caducous but rarely persistent at the terminal bud, about 5 mm. long, attenuately awl-shaped, brown, ventrally glabrous, dorsally strigose. Leaves deciduous, membranous, 5 to 10 or rarely 15 cm. long, 3 to 6 or rarely 8 cm. broad, narrowly ovate or oblong in outline, obtuse, cuneate or unequally somewhat rounded, deeply incised with narrow rounded open or rarely closed sinuses forming 5 or 6 or sometimes even 9 oblong entire rounded or rarely acute lobes, the incisions reaching two-thirds or three-fourths the distance to the midrib or those near the base and apex

quite shallow, margins minutely cartilaginous or subrevolute, upper surface lustrous dark green, glabrous or sparsely minute-stellate- or simple-pubescent, lower surface dull, lighter green or somewhat canescent, rather densely minute-stellate or simple-pubescent or subglabrate, densely microscopically raised-white-punctate; veins as many as the lobes and passing into them and with occasional branching intermediates, minutely raised (including the ultimate reticulum) on both surfaces, somewhat more prominent beneath; petioles 12 to 17 or even 22 mm. long, 0.5 to 1.0 mm. thick, red especially toward the bases, densely short-stellate- or simple-pubescent. Catkins? Fruit annual, solitary or paired, subsessile or on peduncles 3 to scarcely 5 mm. long and 2 mm. thick; cups hemispheric, about 15 to 17 mm. broad and 10 mm. high, margins thin and flat, scales oval, acute, basally somewhat thickened, more or less densely puberulent except the apices which are sometimes nearly glabrous and brown; acorns about 15 mm. long and 12 mm. broad, broadly ovoid, dull light brown, glabrous, about one-half included.

CHIHUAHUA: Mun. de Madera, Garabato, Sept. 27, 1939, C. H. Muller 3535 (USNA—type); C. H. Muller 3535A (USNA); west of Chihuahua, August 29, 1936, H. LeSueur 523 (Mu, T); Sept. 30, 1939, C. H. Muller 3582 (USNA).

Quercus albaefolia is closely related to *Q. Gambelii* Nutt. from which it is distinguished by its larger leaves and much larger fruit.

Quercus albaefolia is rather common in moist arroyos in open or dense pine forest of the Sierra Madre in western Chihuahua. It is not a vigorous or gregarious species and therefore occurs singly or as a few small trees in a natural clearing in the pines. The specific name is purposely spelled with the *ae* connective and does not constitute an orthographic error. The name is intended to call attention to the resemblance of the leaf size and shape to that of *Q. alba* of the Eastern United States.

***Quercus derrumbaderoensis* nom. nov.**

Quercus reticulata f. *pungens* C. H. Muell., Journ. Arn. Arb. 17:166. 1936.

A low shrub intricately branched and reaching a height of 2 m. Twigs about 1 mm. thick, terete, densely yellow-stellate-tomentose, the second year nearly glabrate or somewhat puberulent, brownish-gray with sparse inconspicuous lenticles. Buds about 1.5 mm. in diameter, subspheroid, shiny reddish-brown, glabrous. Stipules caducous, about 3 or 4 mm. long, ligulate, straw-colored, glabrous on the ventral side and sparsely pilose dorsally. Leaves deciduous, rather thick and leathery, 15 to 30 mm. long, 6 to 14 mm. broad, ovate or elliptic to oblong in outline, acute, obtuse, or rounded at the apex, shallowly cordate at the base, irregularly undulate or pungently toothed especially toward the apex, the teeth mucronate, margins irregularly crisped and cartilaginous-revolute, upper surface dull green, sparsely yellow-stellate with fine crisped hairs, lower surface densely yellow-tomentose with the same type of hairs, the blade smooth beneath the detachable tomentum; veins about 6 to 8 on each side, slightly impressed above and very prominent beneath, the reticulum slightly raised on both surfaces; petioles 3 to 4 mm. long, densely

yellow-tomentose. Catkins? Fruit annual, 1 to 3 on a densely tomentose peduncle 5 to 10 mm. long; cups hemispheric, about 12 mm. broad and 6 mm. deep, the margins thin, scales broadly triangular, the bases thickened and densely woolly (especially those near the base of the cup), the apices thin, appressed, narrowed but rounded, glabrous and reddish-brown except the ciliate margins, the apices especially prominent near the margins of the cup; immature acorns rounded, light straw-brown, glabrate except about the style bases, probably not half included at maturity.

NUEVO LEON: Mun. de Derrumbadero, Hac. San José de Raices, above San Enrique, August 6, 1935, C. H. Mueller 2417 (AA—type as of *Q. reticulata* f. *pungens*).

Quercus derrumbaderoensis is rather closely related to *Q. microphylla* Née of Guanajuato and Hidalgo on the southern plateau. From that species it is distinguished with difficulty by its cordate leaves with veins less prominent beneath, prominent teeth with obvious mucrones, and its smaller glabrous shiny buds. These differences, though scarcely obvious and requiring close inspection, are nevertheless of considerable importance. This species is of very local occurrence, having been encountered in only one canyon far isolated from any related species. Its tentative reference to *Q. reticulata* has proven wholly unwarranted.

The species occurs abundantly as a constituent of the chaparral in a dry open canyon at about 2,400 m. altitude on the xeric west slope of the Sierra Madre Oriental. It is confined more or less to the rough topography of rocky (limestone) arroyo banks.

Quercus Edwardsae sp. nov.

Ramuli 2 mm. crassi, glabrati vel sparse stellato-furfuracei, folia decidua, 8-10 cm. longa, 3-5 cm. lata, oblonga vel anguste obovata, basi rotunda vel subcuneata, apice acuta, ad apicem paucidentata, ceterum integra, utrinque glabrata, venis utrinque 8-9 subtus prominentibus, petioli 10-15 mm. longi, glabri, fructus annuus, solitarius vel binus brevipedunculatus.

Twigs rather slender (2 mm.), hardly fluted, transiently sparse-stellate, light brown with numerous very salient white lenticels, becoming grayish the second year with the lenticels even more prominent. Buds ovoid, obtuse, scarcely 3 mm. long, 2 mm. broad, dull brown, sparsely pubescent, the linear pubescent stipules caducous. Leaves deciduous, 8 to 10 cm. long and 3 to 5 cm. broad, oblong to very narrowly obovate, the base rounded to usually subcuneate, the apex acute, entire save for several irregular mucronate-tipped antrorse teeth near the apex, glabrous on both surfaces or very sparingly stellate near the midrib beneath, the upper surface shiny, the lower dull green; veins about 8 or 9 on each side with few intermediates, passing into the teeth when those are present, irregularly branched and occasionally looping, quite prominent beneath, scarcely impressed above, the reticulum very prominent beneath; petioles 10 to 15 mm. long, 1 to 1.5 mm. thick, glabrous. Catkins? Fruit annual, solitary or paired, sessile or usually subterminal on densely

short-hairy peduncles 1 cm. long or more; young cups hemispheric, the tightly appressed scales narrowly rounded, minutely dense-hairy save the smooth margin; acorns?

NUEVA LEON: near Lampazos, June 27, 1937, *M. T. Edwards* 435. (Mu—type).

Quercus Edwardsae is closely related to *Q. porphyrogenita* Trel. from which its large oblong leaves with antrorse mucronate teeth distinguish it.

Quercus filiformis sp. nov.

Frutex parvus, procumbens, ramuli 0.4-1 mm. crassi, sparse stellato-pubescentes vel glabrati, folia decidua, 10-45 mm. longa, 4-15 mm. lata, oblonga, apice acuta vel obtusa, basi cuneata vel rotundata, integra vel crasse dentata, supra glabra et nitida, subtus minute puberulenta, venis utrinque 6-8 anastomosantibus atque prominentibus, petioli 1.25-2.5 mm. longi, sparse stellato-pubescentes vel glabrati.

Low sprawling shrub to 3 dm. tall and twice as broad, irregularly and openly branched. Twigs 0.4 to 0.6 or rarely 1 mm. in diameter, minutely fluted or subterete, brown, sparsely short-stellate or glabrate, becoming gray the second season with few relatively large raised lenticels. Buds 1 to 2 mm. long, broadly to narrowly ovoid, light brown and sparsely pubescent about the apex. Stipules caducous except those about the terminal bud, about 2 or 3 mm. long, ligulate but strongly concave ventrally especially toward the obtuse apex, brown, glabrous except the ciliate and dorsally pubescent apical end. Leaves deciduous, thin and hard, 10 to 25 or on vigorous branches 45 mm. long, 4 to 7 or rarely 15 mm. broad, oblong, acute or obtuse, mucronate-tipped, unequilaterally rounded or sometimes subtruncate or subcuneate, entire or an occasional mucronate tooth near the apex or profoundly toothed or lobed particularly near the apex, margins somewhat crisped, slightly cartilaginous, scarcely revolute, upper surface rather shiny green, glabrous, lower surface dull glaucous green with minute sparse simple hairs and microscopically abundantly white-punctate; veins about 6 to 8 on each side with some intermediates, much branched and obviously anastomosing, the principal branches passing into the mucronate teeth where those are present, somewhat prominent (even to the reticulum) on both surfaces or only the principal secondaries raised; petioles 1.25 to 2.5 mm. long, 0.2 to 0.5 mm. thick, red or brown especially toward the bases, sparsely short-stellate or glabrate. Catkins and fruit?

Quercus filiformis is an off-shoot of the series *Opacae* with rather extreme characters to be included in that series. The nearly procumbent habit and exceedingly slender twigs and petioles very clearly distinguish *Q. filiformis* from *Q. Pringlei* v. Seem. to which it is most closely related.

Q. filiformis occurs very sparsely in densely shaded moist canyons in pine-oak forest. Probably no other clearly distinct species of oak is so utterly insignificant in any but a phylogenetic sense. It apparently produces no stems as much as a centimeter in diameter and grows so openly and so sparsely as

to be of practically no watershed control value, and it is clearly restricted to the dense shade of well forested arroyos.

COAHUILA: Mun. de Cuatro Ciénegas, Sierra de la Madera, Cañon del Pajarito, Sept. 5, 1939, C. H. Muller 3150 (USNA—type).

Quercus Gentryi sp. nov.

Arbor grandis, ramuli 1-2.5 mm. crassi, glabrati; folia tarde decidua, 5-11 cm. longa, 1.5-2.5 cm. lata, anguste lanceolata, apice acuta vel longe acuminate, basi rotunda vel subcuneata, integra, supra glabra et nitida, subtus minute puberulenta, venis utrinque 15-25 anastomosantibus, supra impressis, subtus prominentibus, petioli 5-11 mm. longi, fructus annuus, solitarius, brevipedunculatus, cupula 15 mm. lata, 10 mm. alta, margine invaginata, glans 2/3 inclusa.

Large tree. Twigs 1 to 1.5 or even 2.5 mm. thick, distinctly fluted, dull reddish-brown, glabrous or sparingly stellate-pubescent about the ends, the small light lenticels quite prominent, becoming grayish with more and larger lenticels. Buds about 4 mm. long and 2 mm. broad, acute, narrowly ovoid, shiny brown, glabrous or the scales markedly ciliate; stipules caducous. Leaves persistent at least until spring, thin, 5 or usually 8 to 11 cm. long, about 1.5 to 2.5 cm. broad, narrowly lanceolate, the apex long-acuminate or simply acute, the base unequally rounded to subcuneate, entire, the margins minutely cartilaginous, flat or minutely revolute, upper surface somewhat shiny, dark green, glabrous except at the base of the midrib, lower surface dull, inconspicuously bullate-granular, apparently glabrous except for the tomentose midrib but the lamina microscopically puberulent with appressed simple hairs; veins about 15 to 20 or 25 on each side and sometimes with secondary intermediates, much branched and obviously anastomosing toward the margin, not prominent above and the principal ones slightly impressed, very prominent beneath but the reticulum merely raised; petioles 5 to 10 or 11 mm. long, sparsely stellate-pubescent or glabrous, yellowish- or reddish-brown. Catkins? Fruit biennial, solitary, peduncles 2 to 4 or 5 mm. long, about 3 mm. thick, glabrous, with prominent lenticels; cups about 15 mm. broad, 10 mm. high, hemispheric or deeper, the bases rounded, margins thickened and inrolled, the scales narrow, rounded, thin, appressed, minutely puberulent, light brown; acorns broadly ovoid to round, about 1 cm. broad and scarcely longer, light brown, minutely puberulent, two-thirds or more included.

SINALOA: summit of Sierra Tacuichamona [Tehuichama], Feb. 19, 1940, H. S. Gentry 5686 (USNA—type); H. S. Gentry 5686a, with the more narrow and longer-acuminate leaves (USNA).

Quercus Gentryi is suggestive of the series *Salicifoliae* Trel. and particularly *Q. salicifolia* Née. From this series it is amply distinguished by its biennial fruit with thick coarsely inrolled cup margins, its leaves granular beneath, and the much more numerous principal veins. No other species in northern Mexico could possibly be confused with *Q. Gentryi* unless it be *Q. ignaciensis* whose short petioles and leaves much narrowed basally clearly indicate its relationship to the series *Acatenangenses* rather than to *Q. Gentryi*.

Quercus ignaciensis sp. nov.

Ramuli 1-1.5 mm. crassi, flavi-stellato-pubescentes, glabrati, folia semper-virentia, 11-13 cm. longa, 2.5-3.5 cm. lata, anguste oblongo-oblancoolata, acuminata, basi anguste rotundata vel cordulata, integra, glabrata, venis utrinque 15-20 anastomosantibus, supra impressis, subtus prominentibus, petioli 2-3 mm. longi, glabrati.

Twigs very slender (1-1.5 mm.), markedly fluted, from sparingly yellow-stellate glabrescent the second year, gray, with scarcely evident lenticels. Buds?, the shedding scales brown and glabrous save the stellate apices and ciliate margins, the stipules persistent. Leaves evergreen, 11 to 13 cm. long, 2.5 to 3.5 cm. broad, narrowly oblong-oblancoolate, the apex very acute or very narrowly rounded, basally narrowed, unequally rounded or subcordate, entire or very obscurely wavy-margined and crisped, minutely but markedly cartilaginous-revolute, red and very sparingly short-stellate on both surfaces when unfolding, soon glabrous, the upper surface green and somewhat shining, the lower more dull; veins 15-20 on each side, often with intermediates, much-branched and obviously looping, impressed above but the midrib and reticulum slightly prominent, the midrib, veins, and reticulum very prominent beneath; petioles 2 to 3 mm. long, from short-stellate soon glabrate. Flowers and fruit?

SONORA: La Silla Mts., Sierra Madre, 25 mi. S. E. of San Ignacio, at 3,700 feet elevation, February 26, 1938, H. T. Green without number (ANS—type).

Quercus ignaciensis is suggestive of *Q. flagellifera* Trel. of Guatemala to which it is quite apparently related. The presence as far north as Sonora of a representative of this markedly tropical group is rather surprising since apparently no members of the series are known in the intervening tropical areas of southern Mexico. *Q. ignaciensis* may be distinguished from *Q. flagellifera* by its entire, somewhat broader, basally less attenuate, and apically shorter-pointed leaves with reticulum very prominent beneath. The character of the venulation is probably the most fundamental distinction.

Quercus Knoblochii sp. nov.

Arbor mediocris, ramuli 1.5-3 mm. crassi, tomentulosi, folia tarde decidua, 6 cm. longa, 2 cm. lata, coriacea, oblonga, apice acuta, basi cordata, ad apicem crasse dentata, puberulenta, supra nitida, venis utrinque 8-9, fructus annuus, brevipedunculatus, parvus.

Moderate-sized tree to 10 m. tall with a trunk diameter of 0.3 m. Twigs 1.5 to 2 or rarely 3 mm. thick, coarsely fluted, reddish-brown, minutely fulvous-tomentulose and tardily glabrate with numerous rather prominent pale lenticels. Buds about 3 mm. long, narrowly lance-elliptic, acute, tan, sparsely scurfy or glabrate, the stipules early caducous. Leaves deciduous, somewhat thick and leathery, 4 to usually 6 or sometimes 12 cm. long, 1.5 to 2.5 or even 4 cm. broad, oblong, broadest above the middle, acute at apex, deeply cordate or auriculate at base or exceptionally rounded, subentire to coarsely and aristately few-toothed above the middle, margins minutely cartilaginous-revolute, upper

surface shiny and apparently glabrous but minutely and sparsely simple- or stellate-puberulent especially along the midrib, lower surface usually obviously fulvous-puberulent or the simple hairs gray and then less apparent, often with gray stellate tufts in the axils of the veins, somewhat shining; veins about 8 or 9 on each side, issuing from the midrib at an angle of 20 to 30 degrees, branching and anastomosing near the margin but eventually passing into the teeth where those are present, moderately raised (including the reticulum) on both sides; petioles 4 to usually 7 or even 9 mm. long, persistently stellate-scurfy. Catkins? Fruit annual, solitary or paired, subsessile or short-stalked, the peduncle 5 to 15 mm. long, stellate-scurfy, the few lenticels scarcely conspicuous; cups about 6 to 8 mm. broad, 5 mm. high, obconic to deeply cup-shaped, the scales broadly ovate to rounded, flat and very closely appressed, very sparsely pubescent or glabrate, light brown to straw-colored; acorns about 10 mm. long (rarely 9 or 11), 6 or 7 mm. broad, elliptic, rounded to subacute at the apex, brown, rather persistently silky-pubescent, about one-third included.

CHIHUAHUA: Mun. de Madera, 25 mi. southwest of Chihuahupá, on the west slope of the Sierra Madre Occidental, October 2, 1939, C. H. Muller 3600 (USNA—type); Mojarachic, November 14, 1939, I. Knobloch 6057 (USNA); February 8, 1940, I. Knobloch 6062 (USNA).

SONORA: Mun. de Nácore Chico, 32 mi. southwest of Chihuahupá, Chihuahua, on the west slope of the Sierra Madre Occidental, October 2, 1939, C. H. Muller 3603 (USNA); 35 mi. southwest of Chihuahupá, October 3, 1939, C. H. Muller 3607 (USNA).

Quercus Knoblochii is most closely related to *Q. Endlichiana* Trel., and particularly to certain forms of that species in the Sierra Madre Oriental. It is clearly distinguished by its elongate oblong leaves.

Quercus LeSueuri sp. nov.

Ramuli 1-2 mm. crassi, dense stellato-villosi et tarde glabrati, folia decidua, 4-7 mm. longa, 1.5-3 mm. lata, ovata, utroque rotundata, undulato-lobata, utrinque dense stellato-villosa, venis utrinque 6-8, subtus prominentibus, petioli 3-7 mm. longi, villosi, fructus annuus, brevi- vel mediocri-pedunculatus, parvus.

Twigs slender (1-2 mm.), fluted, densely short-stellate-villous, the second year glabrate and gray with inconspicuous lenticels. Buds round, obtuse or slightly acute, glabrous, dark brown and shiny, the short awl-like stipules often persistent. Leaves deciduous, 4 to 7 cm. long, 1.5 to 3 cm. broad, usually rounded at both ends or the base truncate, rounded, or rarely cuneate, margins undulately shallow-lobed, the sinuses directed obliquely backward, dull green above, lighter beneath, both surfaces densely short soft stellate-pubescent with no especial concentration of pubescence in sheltered places; veins 6 to 8 on each side, much branched and occasionally looping, quite prominent beneath; petioles 3 to 5 or rarely 7 mm. long, 1 mm. thick, stellate like the leaves. Staminate catkins? Pistillate catkins 1- to 3-flowered on a hairy peduncle 5 to 20 mm. long and 1 to 1.5 mm. thick or subsessile. Fruit annual, young

cups with obtuse basally thickened and puberulent scales. (Mature fruit not seen.)

CHIHUAHUA: "West of Babicora Station about 35 miles," Salto de Babicora, July 18, 1937, H. LeSueur 1498 (Mu—type).

A small tree of 2.5 to 3 m. "growing in clumps of 3 to 4 trees" on the north exposure of a very moist canyon, altitude 7,500 feet, *Q. LeSueuri* is very similar to *Q. Gambelii* Nutt. from which it differs in its leaves densely pubescent and in its shallow sinuses and shorter petioles.

Quercus pablillensis sp. nov.

Arbor parva, ramuli circa 1.5 mm. crassi, tomentosi vel glabrati, folia decidua, 4-7 cm. longa, 1-2 cm. lata, oblonga, integra, apice acuta vel obtusa et mucronata, basi rotundata vel cordata, sparse stellato-puberulenta, subtus non bullata, venis utrinque 10-15 anastomosantibus, petioli 5-6 mm. longi, fructus biennis, brevipedunculatus, parvus.

Small tree. Twigs about 1.5 mm. thick, fluted, from short-stellate-tomentose glabrate or rather persistently pubescent, reddish-brown with scarcely prominent lenticels. Buds about 2 mm. long, narrowly ovate, acute, glabrous, glossy-brown; stipules caducous. Leaves deciduous, about 4 to 7 cm. long, 1 to 2 or sometimes 3 cm. broad, oblong, mucronately obtuse to acute, rounded to cordulate at base, entire, the margins revolute, upper surface glabrate or sparsely minute-stellate-puberulent, somewhat shining, lower surface persistently minute-stellate, the hairs peculiarly spaced in a stipple effect, the surface rather glossy, not bullate but the ultimate reticulum minutely impressed in the flat surface; veins 10 to 15 on each side, rather irregular and with occasional evanescent intermediates, much branched and anastomosing, slightly impressed above but the reticulum minutely raised, prominently raised beneath, the coarser reticulum slightly so, and the ultimate reticulum (visible only with a lens) minutely impressed; petioles 5 or 6 mm. long, from densely short-tomentose persistently somewhat pubescent. Staminate catkins 3 to 4 cm. long, rather loosely flowered with a densely tomentose rachis, the anthers exserted from the glabrous perianth. Pistillate catkins 5 to 10 mm. long, the tomentose peduncle 1- to 3-flowered. Fruit biennial, subsessile to evidently stalked, the peduncle 2 to 5 or 10 mm. long and 2 mm. thick; cups small, about 10 mm. broad, hemispheric, the base somewhat constricted, scales ovate to oblong, truncate, flat and tightly appressed, puberulent, light brown, acorns (immature) from puberulent becoming glabrate, probably two-thirds included at maturity.

This species was reported as *Quercus mexicana* f. *Bonplandii* Trel. (Muel-ler, Journ. Arn. Arb. 17:172. 1936) which it superficially resembles very closely. However, the flat lower leaf surface of *Q. pablillensis* distinguishes it from *Q. mexicana* and the series *Mexicanae* Trel. which are characterized by leaves strongly bullate-granular beneath. The affinity of *Q. pablillensis* is with the *Mexicanae* rather than any other series.

NEUVO LEON: Mun. de Galeana, Hac. Pablillo, Cañon San Francisco, May 11,

1934, C. H. and M. T. Mueller 308 (AA, Mu); July 19, 1934, C. H. and M. T. Mueller 1100 (AA, Mu—type); August 11, 1936, M. Taylor 141 (Mu); August 21, 1936, M. Taylor 199 (Mu).

Quercus palustris Muench., f. *Nuttallii* (Palmer) comb. nov.

Quercus Nuttallii Palmer, Journ. Arn. Arb. 8:52. 1927.

Few of the widespread species of *Quercus* in the Eastern United States do not exhibit forms which at one time or another have been taken for distinct species. These variants can be referred to one of three categories as follows: (1) segregates which maintain themselves geographically, ecologically, and morphologically distinct—such entities may be regarded as varieties or species, depending upon the degree of their differentiation and the sympathies of the taxonomist; (2) constant site variants without geographic distinctness—such plants are merely forms of their species; and (3) miscellaneous variations which follow no rule and apparently can be correlated with no cause—such plants are worthy of no names but have frequently been the bases of extravagant claims for hybridization in the oaks.

Quercus georgiana Curtis is a geographically and ecologically distinct aberrant of *Q. palustris* which is restricted to the granite outcrops of Georgia and Alabama. In the writer's opinion it represents a sufficient divergence from typical *Q. palustris* to warrant specific segregation and illustrates the first category of variants. *Q. Nuttallii*, representative of the second category, exhibits no geographic or ecological segregation since it occurs with the parent species throughout a large part of the latter's southern range (Mississippi to eastern Texas and southeastern Missouri). The fruit characters which distinguish the form are very striking, but, unfortunately, almost every species in the Eastern United States exhibits similar fructal polymorphism. Taxonomy can hardly be called upon to furnish names for all the genetic segregates of a highly heterozygous oak population. The third class of aberrants scarcely merits discussion. A little more assiduous application on the part of the casual students of *Quercus* would greatly decrease the number of so-called hybrids which are perennially being stillborn on herbarium labels.

Quercus sierramadrensis nom. nov.

Quercus tenuiloba f. *gracilis* C. H. Muell., Journ. Arn. Arb. 17:178. 1936.

Twigs slender (1-2 mm.), fluted, quickly glabrate and dull reddish-brown with few inconspicuous lenticels, the second year still prominently fluted, gray. Buds ovoid, 2 to 3 mm. long, 1 to 2 mm. thick, straw-colored, glabrous and shiny; the stipules caducous. Leaves deciduous, 10 to 15 or 18 cm. long and 2 to 4 cm. broad, oblanceolate, the apex acute, the base cuneate or somewhat rounded, the margins minutely cartilaginous-revolute, rather saliently aristate-dentate with moderate rounded sinuses save at the entire base, glabrate and glossy save a slight stellate pubescence along the midrib beneath particularly in the axils of the principal veins, the lower surface somewhat coppery; veins about 8 or 10 on each side with occasional intermediates, passing into the teeth where those are present, slightly impressed above and prominent

beneath, the reticulum very prominent beneath; petioles about 3 to 4 mm. long, 1.5 mm. thick, glabrate. Catkins and fruit unknown.

NUEVO LEON: Mun. de Villa Santiago, Las Adjuntas, in the Sierra Madre Oriental, June 25, 1935, C. H. Mueller 2048 (AA—type as of *Q. tenuiloba* f. *gracilis*).

Quercus sierramadrensis is a slender, rather small tree reaching about 10 m. in height, growing in moist, densely shady situations at an altitude of about 1,500 m. This species probably has a very local distribution since it was not found in any other of the many canyons of the Sierra Madre in the course of intensive field study of the oaks both to the north and to the south. This species is undoubtedly related to *Q. tenuiloba*, but it now seems that the relationship cannot be conspecific. *Q. sierramadrensis* is distinguished by its narrowed leaf bases (neither truncate nor cordate) and very short petioles.

Quercus supranitida nom. nov.

Quercus revoluta f. *acuta* C. H. Muell., Journ. Arn Arb. 17:166. 1936.

Twigs slender (1 to 1.75 mm.), from densely yellow-stellate-tomentose glabrate the second year and gray with few scarcely evident lenticels. Buds ovoid, obtuse, scarcely over 1.5 mm. long and 1 mm. broad, reddish-brown, the scales glabrous save the markedly ciliate margins; the short subulate stipules soon caducous. Leaves deciduous (?), small (3 to 5 cm. long and 1 to 2 cm. wide), oblong to lance-elliptic, acute, the base truncate, rounded, or subcuneate, entire or shallowly few-toothed and mucronate above the middle, the margin decidedly revolute but irregular or slightly crisped, upper surface somewhat shining, sparsely roughened with short stellate hairs, the principal veins slightly impressed but the reticulum raised, lower surface yellow-stellate-tomentose with the veins quite prominent, the midrib tending to be glabrous; veins about 8 or 10 on each side, much branched and anastomosing or simple if passing into the teeth; petiole 2 or 3 mm, densely tomentose. Staminate catkins? Pistillate catkins of 1 to 4 or 5 flowers subsessile or on a peduncle about 5 mm. long. Young cups subsessile, the scales reddish-brown, ciliate or puberulent on the back. Mature fruit not seen.

NUEVO LEON: Mun. de Galeana, Puente de Diós, July 12, 1935, C. H. Mueller 2169 (AA—type as of *Q. revoluta* f. *acuta*).

The tardily glabrate twigs, somewhat smaller leaves, only slightly impressed veins, and subsessile cups of *Q. supranitida* distinguish it from *Q. revoluta* Trel. under which it was described as a form. It is now quite clear that the two plants are not conspecific, and it seems that they can scarcely be referred to the same series.

Quercus supranitida is related to *Q. microphylla* Née from which it may be distinguished by its larger and less tomentose leaves. Née's description of *Q. microphylla* characterizes that species so as to suggest quite strongly the more northerly *Q. intricata* Trel. The description of *Q. microphylla* in Trelease's monograph is much more suggestive of *Q. supranitida* which clearly

is unlike either *Q. intricata* or *Q. microphylla* in size and texture of leaves and pubescence.

Quercus tamiapensis sp. nov.

Ramuli 1.5-2.5 mm. crassi, tomentosi, tarde glabrati, folia tarde decidua, coriacea, 6-9 cm. longa, 2-4 cm. lata, oblonga vel sub lanceolata vel oblanceolata, ad apicem undulata vel crasse dentata, apice subacuta, basi rotundata vel subcordata, supra sparse stellato-puberulenta vel glabrata, subtus stellato-tomentosa vel glabrata, venis utrinque 10-12 anastomosantibus, subtus prominentibus, petioli 5-7 mm. longi, stellato-tomentosi, fructus annuus, solitarius vel binus, brevipedunculatus, cupula 18 mm. lata, 12 mm. alta, glans $\frac{1}{2}$ inclusa.

Moderate-sized tree with gray bark. Twigs 1.5 to 2.5 mm. thick, scarcely fluted, grayish-yellow with felt-like tomentum, glabrous and gray the second year with scarcely evident lenticels. Buds about 2 mm. in diameter, round or broadly and obtusely ovoid, brown, glabrous or the scales finely ciliate; stipules caducous or persistent about the terminal bud, 5 or 6 mm. long, narrowly ligulate, brown, pubescent. Leaves persistent, at least until spring, thick-chartaceous, about 6 to usually 8 or 9 cm. long and 2 to usually 3 or 4 cm. broad, oblong, sub lanceolate, or oblanceolate, acute or finally obtuse, rounded or unequally subcordate at base, undulate or coarsely toothed particularly above the middle, margins minutely cartilaginous-revolute, upper surface glabrous except along the midrib toward the base or minutely and sparsely stellate, somewhat shining, lower surface from loosely stellate-tomentose becoming glabrous except along the midrib and principal veins or occasionally the blade persistently tomentose, dull light green; veins about 10 or 12 on each side, branching and obviously anastomosing or passing into the teeth where those are present, very prominent beneath including the obvious reticulum, scarcely raised above, the principal veins even slightly impressed; petioles about 5 to 7 mm. long and 1 to 1.5 mm. thick, rather persistently stellate-tomentose or yellowish-brown where abraded. Catkins? Fruit annual, solitary or paired on a hoary peduncle about 1 cm. long; cups about 18 mm. broad and 12 mm. high, hemispheric or deeper, the bases perfectly rounded, margins coarse and thick but smooth, scales much thickened below, obtuse but narrowed at the thin appressed apices, densely puberulent, grayish-brown; acorns not seen, half or more included, judging by the cups.

It is difficult to assign *Q. tamiapensis* to the series *Laxae* without reservations, for the thick coarse rather large cups are not suggestive of that group. Yet the species bears a much greater resemblance to the *Laxae* than to any other series. From all other species in the series *Q. tamiapensis* may be distinguished by its coarse cups with much thickened scales, its short peduncles, and by the obviously toothed oblong leaves.

Q. tamiapensis forms a small or moderate tree on openly wooded, sunny slopes at elevations of approximately 4,000 feet. The type was growing in deep soil.

SINALOA: Puerto á Tamiapā, March 8, 1940, H. S. Gentry 5863 (USNA—type).

Quercus Tinkhami sp. nov.

Arbor parva, ramuli dense stellato-tomentosi, folia decidua, 2-4 cm. longa, 1-2 cm. lata, apice rotunda, basi rotunda vel cuneata, subintegra vel crispodenticulata, supra sparse stellato-puberulenta et nitida, subtus dense breviter stellato-tomentosa, venis utrinque 6-8 anastomosantibus, utrinque prominentibus, petioli 2-3.5 mm. longi, dense tomentosi, fructus annuus, solitarius, cupula 10 mm. lata, hemispherica.

Small tree. Twigs about 1.5 mm. thick, coarsely fluted, densely gray-stellate-tomentose and rather persistently pubescent the second year or glabrate and gray with few raised but scarcely conspicuous gray lenticels. Buds about 2 to 2.5 mm. long, scarcely 1.5 mm. broad, round-ovoid, obtuse, sparsely pubescent, brown, the stipules persistent for a time, about 3 mm. long, subulate, dorsally strigose or glabrate. Leaves deciduous, 2 to usually 3 (or sometimes 4) cm. long, 1 to usually 1.5 or 2 cm. broad, thin but rather hard, ellipsoid to usually narrowly obovate or oblong, broadly rounded at apex, basally rounded or sometimes cuneate, subentire to usually remotely mucronate or low-undulate, margins cartilaginously thickened but not revolute, irregularly crisped, upper surface shiny-bright-green, very sparsely stellate-puberulent near the midrib, lower surface persistently short-stellate-tomentose, the tomentum usually spreading and gray but on vigorous shoots often tightly appressed and exposing the light green leaf surface which then appears nearly glabrate; veins 6 to 8 on each side, branching and anastomosing toward the margins, quite prominent and (with the reticulum) forming a pale raised network on the upper surface, similarly raised on the lower surface but obscured by the tomentum; petioles 2 to 3.5 mm. long, densely gray-stellate-tomentose. Catkins? Fruit annual, solitary, subsessile; the cups about 10 mm. broad, 6 or 7 mm. high, deeply cup-shaped, the scales lanceolate, prominently keeled, the thin appressed apices narrowed and russet-brown in color, the bases canescent-tomentose; acorns (immature) densely silky-pubescent about the apex, probably ovoid and one-half included at maturity.

NUEVO LEON: near Doctor Arroyo, August 25, 1940, F. Shreve and E. R. Tinkham 9686 (AA—type).

Quercus Tinkhami is apparently most closely related to *Q. potosina* Trel. from which its subentire leaves with raised pale reticulum on the upper surface and its smaller cups with prominently keeled scales amply distinguish it.

The pale reticulum is rather suggestive of *Q. alveolata* Trel., but the large leaves of that species with their prominently revolute margins would exclude *Q. Tinkhami*. The polymorphism of the pubescence on the under surface of the leaves is rather confusing, but the spreading tomentum of the smaller leaves is obviously typical rather than the appressed pubescence of vigorous shoots which to a certain extent suggests the unrelated *Q. Vaseyana* Buckl.

Quercus trinidadensis sp. nov.

Frutex, ramuli 1-2 mm. crassi, tomentosi vel glabrati, folia sempervirentia, coriacea, 2-8 cm. longa, 1-4 cm. lata, oblonga vel elliptica vel obovata, apice

obtusa vel rotundata, basi cordata, subintegra vel mucronato-dentata, glabra, venis utrinque 7-8, subtus prominentibus, petioli 2-4 mm. longi, stellato-tomentosi vel glabrati, fructus annuus, pedunculatus, cupula 10 mm. lata.

Shrub 0.3 to 1 or rarely 2 m. tall forming dense colonies by rhizome propagation. Twigs slender (1 or sometimes 2 mm.), fluted, from minutely gray-stellate-tomentose early glabrate and gray or brown with scarcely prominent lenticels, the second year with more salient lenticels. Buds about 1.5 mm. long, broadly rounded, brown, glabrous; stipules caducous or persisting through 2 seasons, 3 to usually 5 mm. long, spatulate, light brown, glabrous. Leaves persistent 2 or 3 seasons, rather thick and leathery, 2 to 8 (usually about 5) cm. long, 1 to 4 (usually about 2 or 2.5) cm. broad, oblong to elliptic or somewhat broader above the middle, obtuse or rounded at apex, cordate at base, subentire to usually repandly or mucronately toothed especially toward the apex, the teeth tipped by blunt callous mucrones, margins cartilaginous but scarcely revolute, upper surface dull green, glabrous except along the midrib toward the base, lower surface similar but glaucouscent; veins 7 or 8 on each side, irregularly branching and inconspicuously anastomosing, passing into the teeth where those are present, scarcely evident above but quite prominent beneath, the reticulum scarcely raised; petioles about 2 to sometimes 4 mm. long, strongly depressed in the basal sinus, dark reddish-brown, yellowish-stellate-tomentose or glabrate. Catkins? Fruit annual, solitary, paired, or several on a stellate or glabrate peduncle 5 to 25 mm. long and 1 mm. thick; cups about 10 mm. in diameter and 5 mm. deep, cup-shaped, the scales moderately thickened basally with short narrow rounded apices, densely canescent except the glabrous red or brown apices; acorns (immature) ovoid, about half included.

NUEVO LEON: La Trinidad, Mun de Montemorelos, on open slopes or in open forests, August 18, 1939, C. H. Muller 2803 (USNA—type—, AA); August 19, 1939, C. H. Muller 2823 (USNA). TAMAULIPAS: San Lucas, June 1930, H. W. Viereck 601 (US).

Quercus trinidadensis is most closely related to *Q. depressipes* Trel. with which it shares the marked depression of the petioles within the basal leaf sinus. It is distinguished from that species by its much larger leaves and distinctly evergreen habit.

QUERCUS: WISLIZENI A. DC., DC. Prodr. 16(2):67. 1864.

The circumstances under which the type locality of this species was determined have never been clearly explained. In the original description De Candolle locates the type as follows: "In montibus mexicanis ad occid. Chi-huahuae prope Cosiquiriachi, alt. 7,000 p." Sargent in the Silva and Trelease in his monograph both state that the Mexican locality is erroneous and that the type was collected in California. Neither offers any explanation of the correction, but it obviously relates to a remark by Engelmann (Trans. Acad. Sci. St. Louis 3:396. 1877) in which he says of *Q. Wislizeni*, "With his usual acumen, A. DeCandolle discovered this species in a small fruiting specimen, brought by Dr. Wislizenus in 1851 from the American Fork of

the Sacramento River, but through a mistake of mine, he located it near Chihuahua."

DeCandolle's description of the leaves of *Q. Wislizeni* strongly suggests another species which grows commonly about Chihuahua, and for that reason Dr. Engelmann's generous assumption of fault seemed in error. Furthermore, not all contemporary botanists appeared willing to accept the Engelmann-Sargent-Trelease disposition of the case. For these reasons the type of *Q. Wislizeni* in the herbarium of the Missouri Botanical Garden was examined together with all other material which might have figured in the original description. The individual peculiarities of the type specimen readily explained the resemblance of the description to another species. There is no doubt that the type is correctly labelled, for it is clearly the Californian species and not the Chihuahuan one. A post-publication annotation, presumably by Engelmann, locates the collection as "near Auburn" on the Sacramento River. The greater part of the label is in De Candolle's script and is signed by him, and he recorded the locality as "California." It therefore seems that Engelmann was not responsible for De Candolle's error in citing the locality but that De Candolle himself made the error, citing a locality from which a large part of Wislizenus' collections were taken.

ULMACEAE

Ulmus montereyensis sp. nov.

Arbor mediocris, ramuli puberulenti, folia coriacea, 2.5 cm. longa, 1-2.3 cm. lata, anguste elliptica vel anguste ovata vel late lanceolata, apice acuta vel rare obtusa, basi rotundata vel subcordata, duplicati-serrata, supra pilis brevibus rigidis asperata, subtus pilosa, venis utrinque 8-10, supra valde impressis, petioli 2-3 mm. longi, flores vernaes, inflorescentia paniculata, 1 cm. longa, glanduloso-puberulenta et pilosa, sepala anguste-obovata vel lanceolata, acuta, integra vel apice divisa, ovarium dense canescens, stigmatibus reflexis.

Twigs 0.8 to 1.2 mm. thick, distinctly fluted, reddish-brown, puberulent and sparsely pubescent. Terminal vegetative buds 2.5 to 3 mm. long and 1 to 1.5 mm. thick, lanceolate to subovoid, acute, the scales dark reddish-brown, sparsely ciliate, minutely puberulent; stipules caducous. Leaves thick and hard, 2 to 4 or even 5 cm. long, 1 to 1.8 or even 2.3 cm. broad, narrowly elliptical to narrowly ovate or broadly lanceolate, markedly acute or a rare individual obtuse, unequilaterally rounded or subcordate, the margins low-serrate with each tooth again obscurely notched, upper surface shiny and dark green, apparently glabrous except along the sunken midrib but scabrous with minute pustules and forward-directed minute harsh hairs, lower surface dull light green, minutely pilose especially on the veins, minutely bullate; veins about 8 or 10 on each side, passing directly into the teeth or branching and passing into two adjacent teeth, markedly impressed above and very prominent beneath; petioles 2 to 3 mm. long, puberulent and pilose like the midrib. Axillary flower buds ovate, at first acute, about 3 mm. long and 1.5 to 2 mm. broad, the scales dark reddish-brown, sparsely ciliate, minutely puberulent or glabrous

and shiny, opening in late summer. Inflorescence a simple panicle about 1 cm. long at anthesis, peduncle and pedicels glandular-puberulent and sparsely pilose, pedicels articulated above or below the middle. Calyx divided nearly to the base into six erect brown sepals, sepals oblanceolate, narrowly obovate or lanceolate, acute, entire or the apices divided into two acute lobes, 1 to 1.5 mm. long and 0.5 mm. broad, sparsely ciliate about the apex. Stamens about 2.5 mm. long. Ovary about 2 mm. long at anthesis, elliptic, densely glandular-puberulent and white-hirsute; stigmas reflexed and adpressed to the young samara margins. Fruit not seen.

NUEVO LEON: Mun. de Monterrey, lower Cañon Diente along arroyo banks, August 11, 1939, C. H. Muller 2670 (USNA—type).

Ulmus monterreyensis is a moderate-sized tree reaching a height of 12 m. with a trunk 0.3 m. in diameter. Although the species is very rare in the type locality, two other specimens were observed growing in small stream valleys between Monterrey and Villa Santiago, and it is said to be quite common in nearby localities. The occurrence of the tree near habitations (at the mill and buildings of a mining company) at first suggested cultivation, and it was suspected that the species might prove to be *U. parvifolia* Jacq. Its close resemblance to *U. crassifolia* Nutt. was also noted. From *U. parvifolia* the new species is clearly distinguished by its white-hirsute ovaries and veins impressed above as opposed to the merely puberulent ovaries and veins not impressed in the Asiatic species. From *U. crassifolia* the new species may be distinguished by its densely hirsute ovary, acute and often acutely bifid sepals, and characteristically acute leaves.

This is the fourth species of *Ulmus* described from Mexico and the third in the eastern mountain ranges. *U. LeSueurii* Standl. is known only in the Rio Bonito area of Sonora (erroneously cited as Chihuahua under the original description). It was described from sterile material, and it is difficult to judge if it may belong to the autumn-flowering group or not. Its generally larger leaves with subulate-mucronate teeth definitely distinguish it from *U. monterreyensis*. *U. divaricata* C. H. Muell., also from Cañon Diente in Nuevo Leon, and *U. multinervosa* C. H. Muell. from Coahuila are both spring-flowering and rather closely related in vegetative characters to *U. americana* L. This, then, is the first definite record of an autumn-flowering species in Mexico, although Standley has surmised with good reason that *U. crassifolia* crosses the border into Tamaulipas from Texas.

BERBERIDACEAE

Berberis eutriphylla (Fedde) comb. nov.

Mahonia eutriphylla Fedde, Bot. Jahrb. Engl. 31:91. 1902.

Fedde's material (*Ehrenberg 1109*) is not now available, and his citation of the type locality as "Kaukando (?) bei la Encarnacion" is not very illuminating. It is impossible to say if the collection of this species in central Coahuila represents an appreciable extension of range or not.

The type collection is completely sterile, and in the recently collected

material only dried peduncles remain. These may be described as simple, 1.5 to 3 cm. long, the bracts much crowded along the distal two-thirds of the axis, ovate, obtuse, rounded or minutely pointed or toothed about the apex, about 1.5 to 2 mm. long. This species occurs as a shrub 2 to 5 dm. tall in moist, shady arroyos. COAHUILA: Mun. de Cuatro Ciénegas, Sierra de la Madera, Cañon del Agua, September 9, 1939, C. H. Muller 3244 (USNA).

Fedde's distinction of *Mahonia* from *Berberis* consists principally of unfavorable criticism of the separating characters which have been proposed. It is difficult to understand why in the face of this evidence he continues to maintain *Mahonia* as generically distinct from *Berberis*.

***Berberis pinifolia* (Lundell) comb. nov.**

Mahonia pinifolia Lundell, Carn. Inst. Wash. Pub. 478:209. 1937.

This species presents an interesting illustration of evolutionary trend. The narrow, revolute leaflets are clearly derived from the broader leaflets of the *Aquifoliatae*. Although the leaves are in some measure suggestive of those of *B. trifoliolata* Moric, the presence of dense cylindrical papillae on the under surfaces clearly denies that relationship. Lundell failed to mention this character although it is clearly evident in an isotype deposited in the Shreve Herbarium at Tucson. In addition to the type collection by Lundell from Charcas, San Luis Potosi, the following are clearly referable here:

ZACATECAS: road 4 mi. south of Cardona toward Sierra Hermosa, September 3-4, 1938, I. M. Johnston 7375 (G); 4 mi. northeast of Villa de Cos on road from Sierra Hermosa to Zacatecas, September 4-5, 1938, I. M. Johnston 7423 (G).

The Zacatecas material agrees with the type collection in having acicular leaflets 3- to 5-palmately arranged on short petioles and the under surfaces densely papillose whenever visible. It differs, however, in one feature of considerable importance in establishing its relationships within the genus. On young, vigorous, basal shoots the leaves are long-petioled, pinnately 5-foliate, and the leaflets are broad and copiously spinosely incised-toothed. This reversion to ancestral form occurs only on what may be termed juvenile material and is a clear case of recapitulation. A similar but clearly different tendency is seen in the following new variety.

***Berberis pinifolia* var. *coahuilensis* var. nov.**

A specie recedit foliis semper palmato-3-foliolatis.

Differs from the species in its leaves always 3-foliate and palmate; leaves on vigorous shoots with slightly longer petioles, palmately 3-foliate, papillose beneath like the species.

COAHUILA: Cañon del Pajarito, Sierra de la Madera, Mun. de Cuatro Ciénegas, September 6, 1939, C. H. Muller 3171 (USNA—type).

This collection, which appears to be a northerly extension of the range of the species, represents a somewhat more advanced stage of evolution from the ancestral pinnate leaf form. The absence of 4- and 5-foliate leaves

and of pinnate leaves even on vigorous young shoots exhibiting broad leaflet blades is taken as indicative of greater advancement in the reduction of leaf surface. The type of this variety was found in sterile condition. It is entirely possible that additional flowering and fruiting material of both it and the typical form of the species will reveal greater differences.

ROSACEAE

CERCOCARPUS MACROPHYLLUS C. Schneid., Handb. Laubh. 1:530. 1905.

This species is known from Jalisco to Veracruz and Querrero. It is recorded here for the first time from NUEVO LEON: top of Sierra de la Cebolla, line between Mun. de Rayones and Mun. de Montemorelos, common in oak scrub on both sides of the ridge, August 21, 1939, C. H. Muller 2930 (USNA).

ANACARDIACEAE

RHUS MICROPHYLLA Engelm. ex Gray in Smithsonian Contr.
3(5):31. 1852.

This species is common throughout western Texas and northeastern Mexico, reaching Arizona, Chihuahua, and Baja California. However, there have been no records from the state of Sonora except the following: Cañon Pulpito (near the Chihuahua line), Mun. de Agua Prieto, October 11, 1939, C. H. Muller 3727 (USNA).

RHUS MUELLERI Standl. & Barkl., Ann. Mo. Bot. Gard.
24:359. pl. 19, fig. 1. 1937.

Heretofore this shrub was known only from the type collection in the mountains above Monterrey, Nuevo Leon. The following record extends its range to COAHUILA: Puerta de San Lazaro, Sierra de San Lazaro (Sierra de la Gavia), Mun. de Castaños, August 31, 1939, C. H. Muller 3089 (USNA).

AQUIFOLIACEAE

ILEX DECIDUA Walt., Fl. Carol. 241. 1788.

Ilex berberidifolia Standl., Field Mus. Bot. Ser. 4:221. 1929.

The type of Standley's species differs in no perceptible degree from *I. decidua* as it occurs along the waterways of southern Texas and in the plateau country of central Texas. It is not remarkable that the species should be found also in the mesic uplands of adjacent Tamaulipas where the type of *I. berberidifolia* was taken. Clearly referable here is a collection from the moist, forested mountain of central NUEVO LEON: between Potrero Redondo and La Trinidad, Mun. de Villa Santiago, August 23, 1939, C. H. Muller 2948 (USNA).

SABIACEAE

MELIOSMA ALBA (Schlecht.) Walp., Repert. Bot. 2:816. 1843.

This tree was known only from the vicinity of the type locality, Jalapa,

Veracruz. A sterile specimen identified by Mr. Paul C. Standley of the Field Museum extends its range to NUEVO LEON: arroyo below Potrero Redondo. Mun. de Villa Santiago, August 15, 1939, C. H. Muller 2710 (USNA, F).

Meliosma alba is locally an important timber tree, but it is rapidly being depleted. Specimens up to 50 feet in height and 4 feet in diameter were observed in several moist canyons in the vicinity of Potrero Redondo. Felled trees are sawed by hand into timbers about 8 by 10 inches and about 5 feet in length. As late as 1935 these were hauled a distance of 15 miles over narrow mountain trails on miniature four-wheeled carts drawn by oxen. In 1939 the timbers were being packed over the same trails on burros. The wood is used in Villa Santiago in the manufacture of furniture for which it is said to be highly prized. The tree is known locally as *ayón*.

LOASACEAE

Eucnide xylinea sp. nov.

Herba perennis, omnino albo-viscido-villosa, floribus exceptis, ramuli 15-18 cm. longi, ascendentes vel appressi, folia 8-11 mm. longa, 4-7 mm. lata, apice obtusa, basi cuneata, 2- vel 4-rotundato-lobata, petioli 5-12 mm. longi, pedunculi 10 mm. longi, accrescentes, flores solitarii, hypanthium subhemisphericum, 5 mm. latum, sepala 7-9 mm. longa, lineari-lanceolata, acuta, petala 15 mm. longa, 5 mm. lata, oblanceolata, apice rotundata, partim puberulenta vel villosa, flava, stamina circa 30, filamenta 12-25 mm. longa, glabra, stylus 30 mm. longus, gracillimus, stigma capitatum, capsula rotunda, 6-7 mm. crassa, semina oblonga vel pyriforma, 0.6-0.7 mm. longa, 0.3 mm. lata, longitudinaliter vix spiralliter 7- vel 9-sulcata.

Perennial herb forming mats on vertical cliffs; densely viscid-white-villous throughout except the lignified bases of old stems and the flowers as described below, the simple hairs completely obscuring the minutely glochidiate pubescence. Stems 15-18 cm. long, more or less erect but appressed to the cliff-face, very brittle. Leaves petioled throughout, the petioles 5 to 12 mm. long; blades ovate, 8 to 11 mm. long, 4 to 7 mm. broad, obtuse, cuneate, roundly 2- to 4-lobed. Flowers solitary, lateral or terminal; peduncles about 10 mm. long at anthesis, accrescent to 18 or 25 mm. in fruit; hypanthium cup-shaped, about 5 mm. in diameter; sepals 7 to 9 mm. long, linear-lanceolate, acute, less densely villous than the vegetative parts; petals about 15 mm. long, about 5 mm. broad, oblanceolate, rounded at the apices, puberulent or scantily villous, particularly on the outer surface above the middle, and glabrate below, lemon-yellow fading to white; stamens about 30, glabrous, the filaments 12 to 25 mm. long, anthers round, about 0.6 mm. in length and breadth; style about 30 mm. long, very slender, glabrous, stigma capitate, scarcely swollen. Capsule globular, about 6 or 7 mm. in diameter, the calyx lobes withering with the petals but the hypanthium remaining green until dehiscence. Seeds oblong or pyriform, 0.6 or 0.7 mm. long, about 0.3 mm. in diameter, longitudinally 7 to 9 grooved and sharply ridged, the grooves scarcely if at all spiralled.

COAHUILA: Mun. de Sierra Mojada, Cañon de San Salvador (above Esmeralda) in the Sierra Mojada, September 14, 1939, C. H. Muller 3311 (USNA—type).

The strictly solitary flowers, small leaves, densely villous-canescens herbage, and the inconspicuousness of the armed hairs so markedly set off *E. xylinea* from any other species of that genus that some doubt was felt in placing it there. However, the lack of any floral scales definitely excludes this species from *Loasa*, the only other genus which seems at all possible for it. Its habit, floral structure, and seed characters are so definitely those of *Eucnide* that no practical purpose would be served by segregating it as a distinct genus.

OLEACEAE

FORESTIERA NEOMEXICANA A. Gray, Proc. Amer. Acad. 12:63. 1876.

Although this species is quite common in New Mexico and Trans-Pecos Texas, it apparently is known in Mexico only from the following records in COAHUILA: Cañon del Agua, Sierra de la Madera, Mun. de Cuatro Ciénegas, September 9, 1939, C. H. Muller 3231 (USNA); Sierra del Pino, Mun. de Ocampo, August 22, 1940, I. M. Johnston and C. H. Muller 593 (AA, USNA).

Fraxinus Greggii A. Gray, f. *nummularis* (M. E. Jones) comb. nov

Fraxinus nummularis M. E. Jones, Contr. West. Bot. 12:59. 1908.

In a previous paper¹ the author concurred with Standley² in his statements concerning *F. nummularis*: "It seems probable that this is a form of *F. Greggii*, bearing the same relation to the latter that *F. dipetala trifoliolata* does to *F. dipetala*. In the type collection of *F. nummularis* all the leaves are simple and oval. A specimen from Sierra de Parras (*Purpus* 5064) shows leaves of the same kind, but some of the leaves are trifoliolate, and some of the simple ones are exactly like the leaflets of *F. Greggii*." This concurrence was prompted by the examination of a series of specimens of *F. Greggii* Gray from the Chisos Mountains of western Texas in which simple, trifoliolate, and 5- to 7-foliolate leaves occurred on a single specimen.

Recently a large series of collections has been made in western Coahuila (including the type locality of *F. nummularis*), adjacent Chihuahua, and western Texas. This series contains some specimens clearly representative of Jones' form and a great many intermediates between that form and *F. Greggii*. It seems that the f. *nummularis* is a response to xeric conditions resulting in reduced leaf segments and shorter, relatively broader, and much thicker blades. The extreme form is found in the vicinity of Sierra Mojada, Coahuila, while radiating out from this the plants became progressively more like *F. Greggii* as it occurs in Nuevo Leon. The western Texas plant is an intermediate with much the aspect of typical *F. Greggii*. The following specimens are representative of the series:

¹ Mueller, C. H., *Torreya* 34:40. 1934.

² Standley, P. C., *Contr. U. S. Nat. Herb.* 23:1135. 1924.

Typical of the species—NUEVO LEON: Mun. de Villa Santiago, between Potrero Redondo and Las Adjuntas, August 24, 1939, C. H. Muller 2596 (USNA).

Intermediate—TEXAS: Terrel Co., 4 miles east of Sanderson, September 25, 1940, I. M. Johnston and C. H. Muller 1451 (AA, USNA). COAHUILA: Sierra del Pino, August 20, 1940, I. M. Johnston and C. H. Muller 387 (AA, USNA).

Typical of *f. nummularis*—COAHUILA: "Sierra Mojada Mts.," April 19, 1892, M. E. Jones without number (US—type); Mun. de Sierra Mojada, Sierra Mojada, Cañon de San Salvador (above Esmeralda), September 14, 1939, C. H. Muller 3309 (USNA); Sierra Almagre, above Rancho El Almagre, September 11, 1940, I. M. Johnston and C. H. Muller 1218 (AA, USNA).

POLEMONIACEAE

COBAEA PRINGLEI (House) Standl., Contr. U. S. Nat. Herb.
17:457. 1914.

This species has been known heretofore only from the type collection near Monterrey, and the following collection extends its range only about 50 miles south along the Sierra Madre Oriental of NUEVO LEON: trail from La Trinidad up the Sierra de la Cebolla, Mun. de Montemorelos, August 20, 1939, C. H. Muller 2876 (USNA). The plant is quite common trailing over shrubs and climbing moderate-sized trees. It was observed also on the opposite (south-west) side of the Sierra.

LOGANIACEAE

EMORYA SUAVEOLENS Torr., U. S., & Mex. Bound. Bot. 121. pl. 36. 1859.

The type of this rare species was collected in the canyons of the Rio Grande below Presidio del Norte, and the species is recorded from Nuevo Leon. It is therefore not surprising to find it also in COAHUILA: Mun. de Castaños, Puerta de San Lazaro, Sierra de San Lazaro (Sierra de la Gavia), August 30, 1939, C. H. Muller 3035 (USNA).

BORAGINACEAE

CORDIA PODOCEPHALA Torr., U. S. & Mex. Bound. Bot. 135. 1859.

This species was described from the vicinity of San Antonio, Texas, and ranges south through Tamaulipas and Nuevo Leon. Its occurrence in Coahuila is to be expected, but apparently it has not been reported. The following collections have been seen from COAHUILA: Soledad, low mountains 25 mi. southwest of Monclova, September 9 to 19, 1880, E. Palmer 1024 (US); in approximately the same area, Mun. de Castaños, Cañon Bocatoche, September 2, 1939 C. H. Muller 3112 (USNA); Mun. de Muzquiz, Sierra de Puerta Santa Ana, Hac. Mariposa, June 23, 1936, F. L. Wynd and C. H. Mueller 240 (US).

SOLANACEAE

PHYSALIS MICROPHYS A. Gray, Proc. Amer. Acad. 21:402. 1886.

Physalis campanulata Brandeg., Univ. Calif. Pub. Bot. 4:278. 1912.

The type of *P. microphysa* was collected by Pringle in the hills about Santa Eulalia, Chihuahua, while the type of *P. campanulata* comes from the

vicinity of San Luis Potosí, S.L.P. Wilkinson's collection of *P. microphysa*, also from the type locality and shortly prior to Pringle's collection of the type, apparently was the only other specimen available at the time of Gray's publication. The great distance between the type localities and Brandegee's emphasis on the campanulate calyx and deflexed fruiting pedicel of the San Luis Potosí form tended to maintain the distinctness of the two proposed species. However, the fruiting calyx of *P. microphysa* is equally as inflated-campanulate, and its pedicels are quite as apt to be deflexed even though Gray failed to mention these points. The dehiscence mentioned by Brandegee is not a true dehiscence but a mere fragmentation and therefore scarcely significant. Duplicates of all three of the above mentioned collections are deposited in the United States National Herbarium.

Another collection clearly referable here was made in COAHUILA: Mun. de Cuatro Ciénegas, Cañon del Pajarito, Sierra de la Madera, September 6, 1939, C. H. Muller 3158 (USNA).

ORCYTES NEVADENSIS S. Wats. in King, Geol. Expl. 40th Par. 5:274.
pl. 28, f. 5-10. 1871.

Watson described the capsule of this species as "membranous," but he said nothing of its dehiscence. Subsequent authors either overlooked Watson's designation of the fruit as a capsule or disbelieved his description. Wettstein (in Engler and Prantl, Die Natürlichen Pflanzenfamilien, Teil 4, Abt. 3b, pp. 10-15. 1895) describes *Orcytes* fruit as a berry. He is followed in this by Tidestrom (Contr. U. S. Nat. Herb. 25:470. 1925) who keys the genus out on the basis of its fruit being a berry.

A collection from Nevada, north of Wadsworth, Washoe County, June 29, 1938, W. A. Archer 6201 (USNA), has an abundance of both young and mature 2-celled fruits. All of the fully grown capsules are thin-membranous-walled, and most of them are dehiscing in a vertical plane perpendicular to the plane of the partition. In a few instances in immature fruits the dehiscence is replaced by a rough fragmentation, but by far the greater number of fruits are mature and dehiscing along a well defined line. *Orcytes*, then, should be keyed out in the family as having a 2-celled capsular fruit, loculicidal or occasionally irregularly fragmenting. In the same material there are a few flowers with six corolla lobes and six functional stamens instead of the usual five of each.

PLANT EXPLORATION AND INTRODUCTION,
BUREAU OF PLANT INDUSTRY,
WASHINGTON, D. C.

Acer glabrum and its Varieties

Allan C. Keller

This study was conducted at the Pomona College Herbarium under the direction of Dr. Philip A. Munz. I am greatly indebted to him for the guidance and assistance which he has given me throughout the study. I am also indebted to the curators of the herbaria from which material was borrowed for this work. These herbaria, with their abbreviations, are as follows:

New York Botanical Garden (NY).
University of California at Los Angeles
(UCLA).

University of California (C).
California Academy of Sciences (CA).
Pomona College (Po).

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History

An investigation of previous studies disclosed a general need for clarifying the various entities connected with *A. glabrum*. One of the earliest attempts to revise the *A. glabrum* group was that of Pax in his revision of Aceraceae (Pax in Engler's Bot. Jahrb. 6:327, 1885, and 7:217, 1886). Pax made the section "Glabra" for this group with two species *A. glabrum* (including a variety *tripartitum*) and *A. Douglasii*, which procedure he also followed a few years later (Engler and Prantl, Die nat. Pflanzenfam., III, 5:272, 1893). But in his treatment of Aceraceae in the Pflanzenreich (IV, 163:45, 1901) he recognized one species with two varieties: *monophyllum* for the less deeply divided and *tripartitum* for the more deeply divided leaves. Such a division gives no recognition to geographical tendencies and does not seem adequate. Such recognition was given by E. L. Greene (Pittonia 5:1-3, 1902), who accepted the validity of *A. glabrum*, *A. Douglasii*, and *A. tripartitum* and proposed for additional species, *A. subserratum*, *A. Torreyi*, *A. diffusum*, and *A. neomexicanum*, but without key or adequate differentiation.

Since that time further definition has been made only by botanists working on the plants of circumscribed geographical areas, so that, aside from the conservative treatment in books like Sargent's Manual of Trees of North America, 682-684, 1922, no additional general treatments have been given for this group.

These local manuals have varied widely in their species concept. For example, *Douglasii* was given specific rank by Piper (Contr. U. S. Nat. Herb. 11:385, 1906), Rydberg (Fl. Rocky Mts., 552, 1917), and St. John (Fl. of S. E. Wash., 252, 1939); varietal rank by Piper (Fl. Palouse Reg., 114, 1901), by Sargent (l. c.); and was not recognized at all by Robinson (in

Gray, Syn. Fl. N. Am. 1:436, 1897) and Howell (Fl. N. W. Amer. 1:117, 1903). Somewhat the same situation has occurred with *tripartitum* and others.

Smiley (U. C. Pub. Bot. 9:261-2, 1921) reviewed some of the earlier work and reduced to varietal rank *Torreyi* and *diffusum* and to synonymy a species proposed by Abrams, *bernardinum* (Torreya 7:219, 1907).

Taxonomic Criteria

In making the present study serious thought has been given to what rank, if any, should be assigned to the various segregates that have been proposed. Since no constant differentiating features have been discovered in floral or fruit morphology and since the only differences observed have been those of leaf-size, -shape, and -division and twig-color, it seemed best to consider these minor and rather variable differences as worthy of varietal rank only. Furthermore each entity maintained in this paper has a fairly definite geographical range with considerable intergradation where their ranges overlap. For example, a specimen was observed to be intermediate between var. *Torreyi* (Greene) Smiley and var. *Douglasii* (Hook.) Dippel, collected at Bear Basin, near Gasquet, Del Norte Co., Calif., Aug. 1-15, 1935, C. and Mrs. Epling (UCLA).

Taxonomic Treatment

ACER GLABRUM Torr., Ann. Lyc. N. Y. 2:172, 1828.

Rounded, glabrous shrub or tree, 2-10 m. tall; twigs reddish-brown, greyish to whitish; petioles reddish, glabrous, 1-9.5 (12) cm. long; leaf blades broadly cordate, 3-5-lobed to 3-parted, truncate to sub-cordate at base, 1.2-13 (16) cm. long, 1.2-11 (18) cm. wide; leaf margin doubly and irregularly serrate, lobes or leaflets cuneate to rhomboid; bud scales tomentose on inner surface, outer pair of bud scales hard, shiny, deep scarlet, 0.5 cm. long, middle rank rose-colored, 1 cm. long and inner pair yellowish, 2-3 cm. long; flowers glabrous, monoecious to dioecious, 0.7 to 1 cm. in diameter, borne in corymbs; length of peduncle plus pedicel 2-7 cm.; stamens 8 (7-9), perigynous, $1/2$ to $5/6$ length of sepals in sterile flowers, much shorter in fertile flowers; sterile flowers staminate, linear petals as long as broader spatulate sepals; fertile flowers perfect, petals $1/4$ to $1/2$ as long as sepals; samara pairs 2-6 (8), glabrous wings overlapping each other to widely divergent (130 deg. angle), 1.5-4.5 (6) cm. long; immature fruits reddish, changing to green and reddish with maturity.

The plant grows at altitudes from 200 (in the Northwest) to 10,400 ft. further south. It grows on rocky north-facing slopes, in canyons, or in damp woods (var. *Douglasii*). Ranges from Alaska to the Rocky Mts. and California and Arizona in a triangular area that includes the Rockies, the Sierras, and the area between. In flower May to June. In fruit May to September.

KEY TO VARIETIES

- A. Samaras not divergent, wing of one overlapping that of the other. Tulare Co., Calif. (g) var. *Greenei*.
- AA. Samaras divergent, wings not overlapping.
- B. Leaf-blades 3-parted, i.e. divided nearly or quite to the base.
- c. Leaf-blades less than 3 cm. wide. W. Wyo. to northeastern Nev. and south-central Utah. (e) var. *tripartitum*.
- CC. Leaf-blades 4 or more cm. wide. Colo., N. Mex., southeastern Utah and southeastern Arizona. (d) var. *neo-mexicanum*.
- BB. Leaf-blades 3- to 5-lobed, usually not divided to the base (except sometimes in *diffusum* and young leaves of *Douglasii*).
- c. Leaf-blades less than 3 cm. wide; twigs usually whitish. W. Utah to eastern and southern Calif. (f) var. *diffusum*.
- CC. Leaf-blades more than 3cm. wide; twigs reddish or greyish.
- D. Leaf-blades 6-11 (18) cm. wide; sinuses between leaf-lobes shallow and open. Alaska to Wyoming and northern border of Calif. (c) var. *Douglasii*.
- DD. Leaf-blades usually less than 6 cm. wide; sinuses 1/3 to 2/3 way to base, narrow.
- E. Leaf-lobes apically rounded in outline; teeth of margin obtuse, short (often 1-2 mm. long). Southern border of Ore. to L. Tahoe region and southern Sierras. (b) var. *Torreyi*.
- EE. Leaf-lobes apically acute; teeth of margin sharply acute, longer (often 2-4 mm. long). Mostly Wyo. and Colo. (a) var. *typicum*.

TREATMENT OF VARIETIES

- a. *Acer glabrum* Torr. var. *typicum* (Wesmael) comb. nov.

Plates 1 and 2, Fig. A.

A. glabrum Torr., Ann. Lyc. N. Y. 2:172, 1828; Torr. & Gray, Fl. No. Am. 1:247, 1838-40; Pax, in Engler's Bot. Jahrb. 7:218, 1886; Sarg., Sylva of No. Am. 2:95, 1891; Sarg., Man. Trees No. Am., 682, 1922; A. Rehder, Man. Cult. Trees and Shrubs, 571, 1927, for lobed forms of Wyo., Colo., New Mex., western Nebr. and Ariz. *A. glabrum* subsp. *typicum* Wesmael, Bull. Soc. Bot. Belgique 29:46, 1890. *A. glabrum* var. *monophyllum* Graf von Schwerin, Gartenfl. 42:650, 1893; Pax in Engler's Pflanzenreich, IV. 163:45, 1901, in part for lobed forms of Wyo., Colo., etc.

Height 3-6 m.; twigs grayish, rarely reddish; leaf-blades broadly cordate, 3- to 5-lobed, truncate to cordate at base, 2-2.5 (6) cm. long, 3-7 (8) cm. wide; petioles 2.7-5 (6) cm. long; middle lobe largest, oblong or broadly cuneate, lateral lobes acute, the teeth sharp, irregular; samara-pairs 2-6 (8) in corymbs; length of peduncle plus pedicel 2-4 cm.; samaras narrowly to widely divergent.

Type locality: "In the Rocky Mountains about latitude 40 deg., Dr. James." Ranging at altitudes of 5500 to 9600 ft. throughout most of Wyoming and Colorado to Arizona, northern New Mexico and western Nebraska. The true *A. glabrum* (var. *typicum*) is commonly 3-lobed, never 3-parted

to the base. In this respect it differs from vars. *neo-mexicanum* and *tripartitum*, which are normally 3-foliate. It is the *A. glabrum* described by Rydberg, Fl. Rocky Mts. and Adj. Plains, 552, 1917, effcept for the 3-foliate form, var. *neomexicanum*.

Representative material of var. *typicum*: Fremont's Second Expedition (NY). WYOMING: Druid Peak, Yellowstone Park, A. & E. Nelson 5786 (NY, Po); Sheridan Co., Big Horn, Tweedy 2645 (NY); Teton Co., Teton Forest Reservation, Brandegee in 1897 (C); Natrona Co., Loomis Creek, Goodding 186 (C, NY, Po); Carbon Co., Little Snake River, Goodding 1713 (C, NY); Albany Co., South Sybille, Nelson 7387 (NY, Po); Sand Creek, Nelson 7006 (NY, Po).—COLORADO: Larimer Co., Rist Canyon, 8 miles west of Ft. Collins, Baker 1493 (Po); Boulder Co., Boulder, Penard 100 (NY); lower Boulder Canyon, Osterhout 8909 (NY, Po); Gilpin Co., Tolland, Overholts in 1914 (NY); Jefferson Co., Bear Creek Canyon, Jones in 1879 (Po); Douglas Co., Genesee Mt., Eastwood 5436 (CA), 5442 (CA), Bethel in 1916 (CA); Fremont Co., Brandegee in 1872-73 (C); El Paso Co., Glen Eyrie, M. E. Jones 41 (Po); San Miguel Co., Norwood Hill, Walker 470 (Po); Pandora, Baker 749 (CA, NY, Po); La Plata Co., La Plata, Baker, Earle & Tracy 672 (NY, Po).—NEBRASKA: Sioux Co., Hat Creek Basin, Webber in 1889 (NY).—UTAH: Cache Co., 4 mi. east of Logan, Maguire 3544 (C); Weber Co., Ogden, Tracy in 1887 (NY); Utah Co., American Fork Canyon, Goodding 1173 (NY, Po); Piute Co., Bullion Canyon, Rydberg & Carlton 7319 (NY).—ARIZONA: Coconino Co., Bill Williams Mt., Rusby in 1909 (NY).—NEW MEXICO: Rio Arriba Co., Haynes Canyon, Alamo National Forest, Barlow in 1911 (UCLA).

b. *ACER GLABRUM* var. *TORREYI* (Greene) Smiley, Univ. Calif. Pub. Bot. 9:261, 1921.

Plates 1 and 2, Fig. B.

A. Torreyi Greene, Pittonia 5:2, 1902. *A. glabrum* of many authors for Sierran form. *A. glabrum* var. *monophyllum* Graf von Schwerin, Gartenfl. 42:650, 1893 for Sierran form.

Height 2-6 m. or more; twigs usually reddish, sometimes grayish; leaf-blades broadly cordate to subreniform, usually 3-lobed (sometimes with 2 additional basal lobes), rarely 3-parted, truncate to cordate at base, 2.5-5 (6) cm. long, 3-5.5 (6) cm. wide; central lobe largest, cuneate, lateral lobes acute, the teeth few to many, usually obtuse; samara-pairs 3-6 (8), in corymbs, length of peduncle plus pedicel 1.7-4 cm.; samaras divergent usually at angle of 45 degrees.

Type locality: "California Sierra at middle altitudes." It ranges at altitudes of 5000-8900 ft. from southern Oregon to southern Sierra Nevada. It resembles closely var. *typicum* of the Rocky Mts., but the leaf-lobes of *Torreyi* are apically rounded with short obtuse teeth, while those of *typicum* are acute, with longer and sharper teeth.

Representative material: OREGON: Josephine Co. above Oregon Caves, Siskiyou Mts., Thompson 12435 (C, CA, NY); Jackson Co., Rogue River Gorge below Eagle Point, Abrams 9883 (Po); Klamath Co., Crater Lake National Park, Heller 13474 (NY).—CALIFORNIA: Camp Agassiz, Eastwood 950 (CA); Del Norte Co., Bear Basin near Gasquet, Epling in 1935 (UCLA), intermediate with var. *Douglasii*; Siskiyou Co., Castle Lake, Eastwood 10728 (CA); Scott Mts. above Callahan, Eastwood & Howell 5018 (CA, NY); Humboldt Co., Trinity Summit, Tracy 5291

(C, Po); Trinity Co., Bear Creek, *Yates 476* (C); Lassen Co., Susanville, *M. E. Jones in 1897* (Po); Plumas Co., Gold Lake Region, *Mrs. Sutcliffe in 1919* (CA); near Long Lake, *Bacigalupi 1659* (Po); 12 miles west of Bucks, *Heller 12054* (CA, NY, UCLA); Sierra Co., Sierra Valley, *Lemmon in 1889* (C); Butte Co., Summit, *Mrs. Bruce 2475* (NY); Jonesville, *Copeland 423* (C, CA, NY, Po, UCLA); Nevada Co., above Donner Lake, *Heller 7043* (C, NY, Po); Placer Co., Emigrant Gap, *Heller 12730* (CA, NY); Eldorado Co., Echo Lake, *Heller 12503* (CA, NY); Calaveras Co., Camp Baxter, north fork Stanislaus River, *Jussell in 1930* (CA); Mariposa Co., Grove of Sequoia gigantea, *Torrey 58* (NY); Yosemite Valley & Mts., *Torrey 158* (NY); Fresno Co., Wood's Creek, *Mrs. Clemens in 1910* (CA, NY, Po); Tulare Co., Bubb's Creek, *Lemmon* (C); Lodgepole Camp, Sequoia Nat. Park, *Darland in 1932* (C, UCLA); Marble Fork of Kaweah River, *Keller 210* (CA, Gray, Po).—NEVADA: Ormsby Co., King's Canyon, *Baker 1054* (C, CA, NY, Po); Lake Tahoe, *Jones in 1927* (Po); Washoe Co., Slide Mt. near Franktown, *Tidestrom 10556* (NY).

c. *ACER GLABRUM* var. *DOUGLASHII* (Hook.) Dippel, Handb. Laubholzkunde 2:438, 1892.

Plates 1 and 2, Fig. C.

A. Douglasii Hook., London Journ. Bot. 6:77, pl. 6, 1847. *A. glabrum* subsp. *Douglasii* (Hook.) Wesmael, Bull. Soc. Bot. Belgique 29:46, 1890. *A. barbatum* Hook., Fl. Bor. Am. 1:113, 1838, not of Michx., 1803. *A. glabrum* Authors for plants from Alaska to northern Wyo. and southern Oregon. *A. subserratum* Greene, Pittonia 5:2, 1902.

Height 1-10 m.; twigs reddish; leaf-blades broadly cordate, sometimes stellate, 5-lobed (divided to 1/3 length of leaf blade) or 3-parted in young shoots, cordate to truncate at base, 5.1-13 (16) cm. long, 6-11 (18) cm. wide; petioles 5-9.5 (12) cm. long; lobes acute, middle lobes largest, sinuses between the leaf-lobes shallow, open, the teeth many, sharp; samara-pairs 2-6 (7) in corymbs, length of peduncle plus pedicel 2.5-4.5 (5) cm.; samaras divergent at angle of 90° or less.

Type locality: "Near springs of the Rocky Mountains about the sources of the Columbia." Ranging at altitudes of 200-7000 ft., from Alaska to northern Wyoming and northern border of California. This northwestern variety often reaches the proportions of a tree and its leaves are commonly much larger than those of the other varieties. Greene recognized as a species *A. subserratum* from a single collection taken near Lewiston, Idaho, *Heller 5089* (C, NY). This collection has unusual serration and is only 3-lobed, but var. *Douglasii* has a number of variations in leaf-size and shape. Material from Alaska appears to have the leaves more star-shaped than does that from farther south; further material may warrant the separation of an Alaskan variety.

Representative material of var. *Douglasii*: ALASKA: Haines, *Anderson 840* (NY); Juneau, *Anderson 535* (NY); Killisnoo, *Eastwood in 1914* (CA).—BRITISH COLUMBIA: near Lillooet, *Macoun 94220* (NY); Hawser Lake, Selkirk Mts., *Macoun 724* (NY); Stikine R., *Walker 123* (CA); Vancouver Island, *M. E. Jones in 1902* (NY, Po).—ALBERTA: near Banff, *Johnson 1223* (NY).—WASHINGTON: Whatcom Co., Razorhorne Creek, Mt. Baker, *W. C. & M. W. Muenscher 5963* (C); Lucia Island, *Zeller 992* (NY, UCLA); Okanogan Co., Oroville, *M. E. Jones in 1911* (Po); Clallam Co., Mt. Washington, *Flett in 1908* (UCLA); Mason Co., Hoodspott,

Piper 1017 (NY); Chelan Co., Stehekin, *M. E. Jones* in 1911 (Po); Lincoln Co., near Sprague, *Sandberg & Leiberg* 156 (C, CA, NY); Kittitas Co., Redtop, *Thompson* 9304 (C, NY); Pierce Co., upper valley of the Nisqually, *Allen* 212 (C, CA, NY); Yakima Co., Wenas, *Griffiths & Cotton* 96 (NY); Kickitat Co., western part, *Suksdorf* in 1884 (CA, NY); Walla Walla Co., Blue Mts., *Piper* in 1896 (C).—OREGON: mts. of eastern Oregon, *Cusick* 3145 (C, NY); Wasco Co., Marion's Pt. Lookout, *G. N. Jones* 4105 (CA); Jefferson Co., base of Mt. Jefferson, *Peck* 9088 (NY); Wallowa Co., Ice Lake Trail, Wallowa Mts., *Eastwood & Howell* 3400 (CA); Baker Co., near Cornucopia, *Thompson* 13410 (C, CA, NY); Baker City, *M. E. Jones* 25357 (CA, Po); Grant Co., Blue Mts., *Henderson* 5478 (CA); Marion Co., near Niagara, *Epling* 5462 (UCLA); Lane Co., Bohemia Mt., *Patterson* in 1926 (C).—IDAHO: Upper Priest River, Boundary Co., *Epling* 7498, 7434, 7163 (UCLA); Priest Lake, *MacDougal* 172 (NY); Lake Coeur d'Alene, *Hitchcock & Samuel* 2630 (CA, UCLA); Slack water, St. Joseph's River, Shoshone Co., *Leiberg* 1292 (C, NY); Lewiston, Nez Perce Co., *A. A. & E. G. Heller* 3089, type coll. subseratum (C, NY); Clearwater River above Lewiston, *Sandberg, MacDougal & Heller* 277 (NY, Po); Seven Devils Mts., Washington Co., *M. E. Jones* in 1899 (Po); Pocatello, Bannock Co., *Donaghe* 40 (CA).—MONTANA: Big Fork, Flathead Co., *Umbach* 172 (NY); Columbia Falls, *Blankinship* in 1899 (NY); McDougal Peak, Lake Co., *M. E. Jones* 8099 (Po); Yellow Bay, *Jones* 8097 (Po); Missoula, Missoula Co., *Kirkwood* in 1910 (CA); Thompson's Falls, Sanders Co., *Hitchcock* 1518 (CA, Po); Alta, Ravalli Co., *Jones* in 1909 (Po); Helena, Lewis & Clark Co., *Butler* 4002 (CA, NY); Bozeman, Gallatin Co., *Blankinship* 105 (C, Po); Livingston, Park Co., *Mrs. Scheuber* 162 (NY).—WYOMING: Mammoth Hot Springs, Yellowstone Nat. Park, *Mearns* 1513 intergrading with var. *typicum* (NY).

d. ACER GLABRUM Torr. var. NEO-MEXICANUM (Greene) Kearney & Peebles, Journ. Wash. Acad. Sciences 29:486, 1939.

Plates 1 and 2, Fig. D.

A. neo-mexicanum Greene, *Pittonia* 5:3, 1902; Wootton & Standley, Contr. U. S. Nat. Herb. 19:411, 1915. *A. glabrum* var. *tripartitum* (Nutt.) Pax, Engler's Pflanzenr. IV, 163:45, 1901 for plants of New Mex., etc.

Height 5-7 m.; twigs grayish or reddish; leaf-blades whitish below, broadly cordate, usually 3-parted, 4.5-7 cm. long, 5-10.5 cm. wide; petioles 4.5-6.5 cm. long; leaflets oblanceolate, acute at apex, the teeth many, sharp; samaras pairs 3-6, in corymbs, length of peduncle plus pedicel 2-3.6 cm.; samaras divergent, usually at narrow angle.

Type locality: "Mountains near Las Vegas, New Mexico." G. R. Vasey in 1881. Range at altitudes of 4000-9200 ft. from Colorado and New Mexico to southeastern Utah and southeastern Arizona. The var. *neo-mexicanum* has been included under var. *tripartitum* by Pax, l. c., but the leaves are larger and the leaflets are whitish underneath and more oblanceolate in shape.

Representative material: UTAH: La Sal Mts., Grand or San Juan Co., *M. E. Jones* in 1913 (Po); Sierra La Sal, *Purpus* in 1899 (C); north slope Abajo Mts., *Goodman & Hitchcock* 1445 (C, CA, NY).—COLORADO: Between Sunshine & Ward, Boulder Co., *Tweedy* 4963 (NY); Headwaters of Clear Creek, Clear Creek Co., *Parry* 338, in 1861 (NY); Buena Vista, Chaffee Co., *Sheldon* in 1892 (NY); Black Canyon, Gunnison Co., *Baker* 124 (C, Po); Paradox, Montrose Co., *Walker* 227 (Po); Pagosa Peak, Archuleta Co., *Baker* 457 (NY, Po); Wootton, Las Animas Co., *Rusby* in 1909 (NY).—NEW MEXICO: mts. east of Santa Fé, *Fendler* 101 (C, NY), *A. A. & E. G. Heller* 3525 (NY, Po); Winsor Creek, San Miguel Co., *Standley*

4036 (NY); Sandia Mts., Bernalillo Co., Jones in 1884 (Po); White Mts., Lincoln Co., *Wooton* 345 (C, NY, Po); 9 miles east of Mogollon, Catron Co., *Wolf* 2717 (C, CA, Po); Lookout Mines, Sierra Co., *Melcalfe* 995 (CA, NY, Po); Sierra Blanca Peak, Otero Co., *Wolf* 2844 (CA, Po); Cloudcroft, *Wooton* in 1899 (NY, Po).—ARIZONA: head of Black River, White Mts., Apache Co., *Goodding* 1205 (NY); Lukachukai Pass, *Eastwood & Howell* 6788 (CA); Mt. Lemmon, Pima Co., *Harris* 16450 (C, NY); Huachuca Mts., Cochise Co., *Goodding* 104 (NY); Chiricahua Mts., *Goodman & Hitchcock* 1196 (C, CA); Monument Peak, *Blumer* 2286 (NY).

e. ACER GLABRUM Torr. var. TRIPARTITUM (Nutt.) Pax, Engler's Bot.
Jahrb. 7:218, 1886; Pax, Pflanzenr. IV, 163:45, 1901.

Plates 1 and 2, Fig. E.

A. tripartitum Nutt. ex Torr. & Gray, Fl. No. Amer. 1:247, 1840. *A. glabrum* f. *trisectum* Sarg., Journ. Arnold Arb. 2:166, 1921; ex Rehder, Man. Cult. trees and shrubs, 571, 1927.

Height 3-6 m.; twigs grayish or whitish; leaf-blades broadly cordate or triangular, usually 3-parted, sometimes 3-lobed, 1.2-3 (3.8) cm. long, 2.6-4 (6.2) cm. wide; petioles 1-3 (3.7) cm. long; leaflets or lobes cuneate, usually obtuse at apex, the teeth few, sometimes only 3 per lobe, to many, usually blunt; samara-pairs 2-5, in corymbs; length of peduncle plus pedicel 2.2-6 (3) cm.; samaras divergent at 45-90 degree angle.

Type locality: "On Bear Ridge, Rocky Mts., lat. 40 deg., near the line of Upper California," collected by Nuttall. Range at altitudes of 5000-10,000 ft., western Wyo. to northeastern Nevada and south-central Utah. This variety refers to the *A. tripartitum* of Nuttall, a 3-foliolate form from the vicinity of the Wasatch Mts. of Utah. Pax in Engler's Bot. Jahrb. 7:218, 1886, includes the *neo-mexicanum* form under *tripartitum*. Sargent, Journ. Arnold Arb. 2:166, 1921, proposed *A. glabrum* forma *trisectum*, stating, "This new name is suggested for the form of *Acer glabrum* Torrey with 3-parted or 3-foliolated leaves, as the name *tripartitum* which has been used for this form of *Acer glabrum* belongs to a little alpine species which Nuttall found," etc. He refers to Pax in Engler's Bot. Jahrb., 1. c. where two specimens are cited under *tripartitum*: the Nuttall one and Fendler 101. If he excludes Nuttall, Fendler 101 would have to be taken as the type number of *trisectum* and would be synonymous with Greene's *neo-mexicanum*. But apparently this usage is not what Sargent intended. On Jan. 2, 1940, Dr. Rehder kindly wrote an opinion, saying, "Apparently Sargent considered *A. tripartitum* Nutt. and *A. neo-mexicanum* Greene as distinct species," i.e., distinct from *A. glabrum*. Since Sargent writes that "the specimens in this herbarium are from the Big Horn Mts. of Wyoming and from those of Utah and Nevada," he apparently refers here largely to what I treat as var. *tripartitum*. Therefore, I place *trisectum* as synonymous to *tripartitum*. Var. *diffusum* sometimes has 3-foliolate leaves but they are smaller than those of *tripartitum*.

Representative material: Bear River, Rocky Mts., Nuttall, type collection (NY). WYOMING: Black Rock Creek, Teton Co., *Tweedy* 342 (NY); Gros Ventre Mts., Sublette Co., E. B. & L. B. Payson 3017 (C, Po); near Cottonwood Lake east of

Smoot, Lincoln Co., *Payson & Armstrong* 3786 (Po).—UTAH: Wasatch Mts., *Watson* 215 (NY); Ogden, Weber Co., *Tracy* 596 (NY); City Creek Canyon, Salt Lake Co., *Jones* in 1880 (Po); Mt. Timpanogos, Utah Co., *Eastwood & Howell* 542 and 469 (CA); Marvinne Laccolite, Sevier Co., *Jones* 5336g (NY, Po); Marysvale, Piute Co., *Jones* 5396 (C, NY, Po); Bryce Canyon, Garfield Co. *Peirson* 7479 (CA).

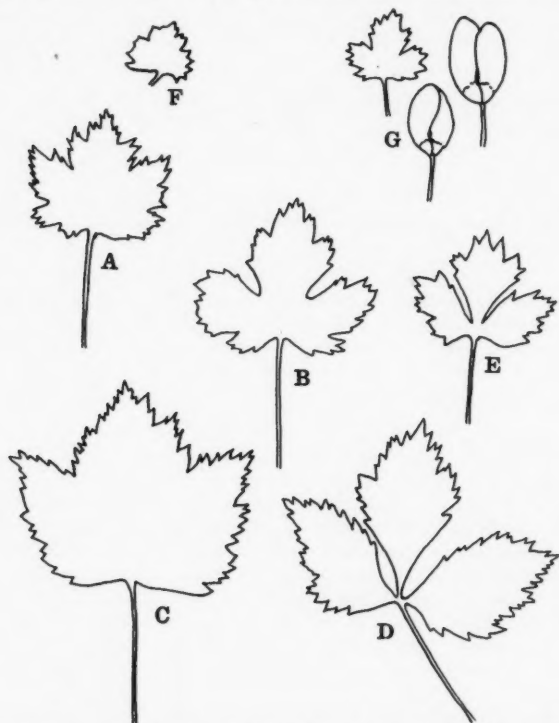


PLATE 1. Leaves of: A. *Acer glabrum* var. *typicum*, drawn from collection by Bethel from Genesee Mt. near Golden, Colo. B. var. *Torreyi*, Eastwood 950. C. var. *Douglasii*, Butler 4002. D. var. *neo-mexicanum*, Blumer 2286. E. var. *tripartitum*, Nuttall. F. var. *diffusum*, Heller 10627. G. var. *Greenei*, Culbertson, under Baker 4678; leaf and fruit. (Drawings reduced one-half.)

f. ACER GLABRUM Torr. var. DIFFUSUM (Greene) Smiley, Univ. Calif.,
Pub. Bot. 9:261, 1921.

Plates 1 and 2, Fig. F.

A. diffusum Greene, Pittonia 5:2, 1902. *A. bernardinum* Abrams, Torreya 7:219, 1907.

Height 3-10 m.; twigs whitish; leaf-blades round to subcordate, 3-lobed to 3-parted, truncate to cordate at base, 1.5-2.5 cm. long, 1.2-2.8 (3.5) cm. wide;

petioles 0.7-1.8 (2.2) cm. long; lobes or leaflets cuneate, obtuse at apex, the teeth few, blunt; samara-pairs 2-5 (6), in cormybs, length of peduncle plus pedicel 1-2 cm.; samaras often widely divergent.

Type locality: "Near the summit of the West Humboldt Mts., Nevada," collected by E. L. Greene. Range: W. Utah to the mts. of central and southern California and northern Arizona. This is a small-leaved shrub with whitish twigs. The leaves are commonly roundish in shape and sometimes 3-foliolate. The San Bernardino and San Jacinto Mt. forms (*A. bernardinum*) seem to be a little different from those farther north, the twigs having more of a grayish white color, but there does not seem to be sufficient difference to merit recognition.

Representative material: NEVADA: Humboldt Canyon, West Humboldt Mts., Humboldt Co., Heller 10627 (CA, NY); Clover Mt. Range near Death, Elko Co., Heller 9161 (NY); Ruby Hill, Jones in 1891 (Po); Aurum, White Pine Co., Jones in 1893 (Po); Comet Peak, Pioche, Lincoln Co., Jones in 1912 (Po); Lee Canyon, Charleston Mts., Clark Co., Heller 11001 (C, NY); Charleston Park, Clokey 5531 (C, CA, NY, UCLA).—UTAH: Gold Hill, Tooele Co., Jones in 1891 (Po); Deep Creek Mts., Maguire and Becraft 2687 (C); 10 miles east of Cedar City, Iron Co., Hitchcock, Rethke, van Raadshooven 4622 (NY, UCLA).—CALIFORNIA: Deer Park, Placer Co., Eastwood 365 (CA); Fallen Leaf Lake, Eldorado Co., Peirson 6267 (Po); near Olancho, Inyo Co., Wolf 1693 (C, UCLA); trail to Big Pine Lakes, Ferris 9008 (C, NY, Po); Birch Creek, White Mts., Duran 3032 (C, CA, Po).



PLATE 2. Distribution of A. *Acer glabrum* var. *typicum*, Wyo., Colo., Utah. B. var. *Torreyi*, Calif., etc. C. var. *Douglasii*, Idaho and northward. D. var. *neo-mexicanum*, Colo., New Mexico, etc. E. var. *tripartitum*, Utah, etc. F. var. *diffusum*, Nevada, etc. G. var. *Greenei*, California.

UCLA); Wild Rose Canyon, Panamint Mts., *Munz 14808* (Po); Whitney Creek, Tulare Co., Culbertson under *Baker 4554* (C, CA, NY); Snow Canyon, San Bernardino Mts., San Bernardino Co., *Parish 5128*, type coll. bernardinum (NY); north slope of Sugar Loaf Mt., *Munz 10778* (C, Po), *Keller in 1939* (C, CA, NY, Po, UCLA); Tamarack Valley, San Jacinto Mts., Riverside Co., *Hall 2602* (C); Tahquitz Peak, *Hoffman in 1929* (Po).—ARIZONA: Kaibab Trail to Roaring Springs, Grand Canyon Nat. Park, Coconino Co., *Eastwood & Howell 1066* (CA).

g. *Acer glabrum* Torrey var. *Greenei* n. var.

Plates 1 and 2, Fig. G.

A. minusculum Greene, ex C. F. Baker, West Am. Pls. 3:3, 1904, nomen nudum; ex Jepson, Silva Calif. 268, 1910 in syn.

Height 2 or more meters; twigs whitish; leaf-blades round to cordate, 3-lobed to 3-parted, truncate to subcordate at base, 1.8-3.1 (5) cm. long, 2.5-4.4 cm. wide; petioles 1.2-4.4 cm. long; lobes or leaflets cuneate to oblong, usually obtuse at apex, the teeth few to many, blunt or sharp; samara-pairs 1-4, in corymbs, length of peduncle plus pedicel 1.7-4 cm.; samaras not divergent, wing of one overlapping that of other.

Planta cum ramis albidis; foliis orbiculatis aut cordatis, 3-lobatis vel 3-partitis, basi truncatis vel subcordatis, 1.8-5 cm. longis, 2.5-4.4 cm. latis; petiolis 1.2-4.4 cm. longis; lobis aut foliolis cuneatis vel oblongis, apices plerumque obtusis; paribus samarum 1-4, in cormybis; samaris non divergentibus, alis imbricatis.

Type, Kern River Tributary, Tulare Co., Calif., Sept. 3, 1904, *Culbertson*, distributed by C. F. Baker, no. 4678; Herbarium of Pomona College no. 136894; isotypes at Univ. of Calif., New York Bot. Garden, Calif. Academy of Sciences. Range, Tulare Co., California. This variety is distinguished by its peculiar fruit; the wings of each pair of samaras overlap each other. In other characteristics the group most nearly resembles *Torreyi*, although some specimens are somewhat like those of var. *diffusum*. Greene, l. c. proposed the name *minusculum*, but no description was ever published.

Specimens examined: CALIFORNIA: Tulare County: Bubb's Creek at South Fork, March, 1906, S. W. Austin (C); vicinity of Mineral King, *Hall & Babcock 5364* (C); head of Kaweah Creek, *Mrs. Derby in 1928* (CA); Topokah Falls, Marble Fork of Kaweah River, *Keller 209* (Po), *211* (CA, NY, Po, Gray).

POMONA COLLEGE,
CLAREMONT, CALIFORNIA.

A Revision of the Celastraceous Genus *Forsellesia* (*Glossopetalon*)

Margaret Ensign

This paper represents an attempt to put some order into the genus *Forsellesia*. The group was studied under the supervision of Dr. Philip A. Munz at Pomona College to whom I am grateful for his assistance and suggestions. I am also indebted to the curators of the herbaria from which material has been available. These herbaria are cited in this paper with the following abbreviations:

Dudley Herbarium of Stanford University.....	DS	Herbarium of the University of California.....	UC
California Academy of Sciences.....	CAS	Herbarium of the University of California at Los Angeles.....	UCLA
Gray Herbarium of Harvard University.....	GH	United States National Herbarium.....	US
Pomona College Herbarium.....	Pom	Arboretum of Department of Agriculture.....	USDA
Rancho Santa Ana Herbarium.....	RAS		

The genus *Forsellesia* was first described as *Glossopetalon* by Gray, *Plantae Wrightianae* 2:29. 1853. However, E. L. Greene discovered that the name was a homonym (*Glossopetalum*, Schreb., *Gen.* 1:205. 1789) and proposed that the group should be given the generic name *Forsellesia*, *Erythra* 1:206. 1893. This name is commemorative of James Henry Forselles, a Swedish mining engineer and botanical writer of the last century. Since Greene's time some authors have used one name and some the other name. Since the International Rules of Nomenclature do not list *Glossopetalon* in the *Nomina Conservanda*, and since they do not recognize orthographic variants (Art. 70, note 4; Greek "petalon," Latin "petalum") I am using the name *Forsellesia* in this paper.

In the past all of the species have been described on the basis of the number of petals and stamens. This study has, however, shown that these characters are variable within a single specimen and that the presence and the character of the stipules and the leaf size and shape form a more sound basis for distinction.

There has always been some doubt as to the taxonomic position of *Forsellesia*. Even Gray who first described the genus under the name *Glossopetalon*, hesitated to place the genus in *Celastraceae* since all of the specimens he was able to examine had flowers with only one carpel. In later collections of *F. nevadensis*, however, particularly those from Titus Canyon in Death Valley, California, I found that flowers possessing two carpels are fairly common. As *F. pungens* also has two carpels there can be no reason for excluding the genus from *Celastraceae* on this basis. The carpels of the other species are

commonly observed to be solitary but even further study may indicate that this is not always the case.

FORSELLESIA (Gray) Greene

- Forsellesia*: Greene, *Erythea* 1:206. 1893; Tidestrom, *Cont. U. S. Nat. Herb.* 25:348. 1925; Wootton and Standley, *Cont. U. S. Nat. Herb.* 19:409. 1915.
Glossopetalon: Gray, *Pl. Wright.* 2:29, pl. 12. 1853; Jepson, *Fl. of Calif.* 2:450. 1936; Munz, *Man. So. Calif. Bot.*, 294. 1935; St. John, *Fl. S. E. Wash. and adj. Idaho*, 250. 1937.
Glossopetalum: Benth and Hooker, *Gen. Pl.* 1(1):368. 1867; Loesener in Engler and Prantl, *Die Nat. Pflanzenfam.* III, 5:219. 1897.

Small deciduous, intricately branched shrubs with slender, greenish, angled, spinescent branches with decurrent lines from the nodes; leaves small, simple, entire, alternate, lanceolate to obovate, pubescent or glabrous, glaucous, veins rather obscure, 2-4 lateral veins parallel to the margin, usually with minute stipules; flowers bisexual, regular or nearly so, usually axillary, borne on slender pedicels with reduced scarious bracts at the base; sepals 5, rarely 4 or 6, hyaline-margined, ovate; petals 5, rarely 4 or 6, white, narrow-oblancoelate, distinct, deciduous, much longer than the sepals, inserted by a narrow base under the edge of a fleshy, crenately 6-10 lobed disk; stamens equal or unequal, the longer ones inserted opposite the sepals; carpels 1-3, distinct, ovate, attenuate to the stigma, sessile upon the disk; ovary superior, 1-celled with 1 or 2 ovules; fruit an asymmetrical ovoid, coriaceous, striated follicle opening along the ventral suture.

Type species, *F. spinescens* (Gray) Greene. The genus apparently grows best in dry limestone regions and ranges from Washington, Idaho, Oregon, southern Utah, and northern Colorado to Arizona and New Mexico, east to Texas and southern Oklahoma and west to Nevada and eastern California.

KEY TO SPECIES

- A. Low matted shrubs, not spinescent, 0.5-2 dm. high; leaves elliptical, unusually thick, ending in a spine; flowers terminal, 5-merous; stamens 10, the 5 opposite the petals as long as the sepals and the 5 opposite the sepals one third longer; carpels 2-3.1. *F. pungens*.
- AA. Intricately branched, usually spinescent shrubs, 1-30 dm. tall; leaves oblong to oblanceolate, thin, acute to acuminate; flowers axillary, 3-6-merous; stamens 4-10, equal or unequal in length; carpels 1-2.
 - B. Young branches very fine, scarcely 0.5 mm. thick; leaves 5-6 mm. long, 1-1.5 mm. wide; flowers 3-5-merous; sepals 1.2-1.5 mm. long; petals 3 mm. long; stamens 4-6. Charleston Mts., Nevada.2. *F. Clokeyi*.
 - BB. Young branches at least 0.5 mm. thick; leaves 5-17 mm. long; flowers 4-6-merous; petals 4-9 mm. long; sepals 1-3 mm. long; stamens 5-10.
- c. Stipules present.
 - D. Stipules more than 0.5 mm. long, frequently adnate to a persistent often glandular thickened base.
 - E. Strongly spinescent, young branches more than 1 mm. thick, becoming yellowish in maturity; stipules less than 1 mm. long. Nevada, Arizona, and California.3. *F. nevadensis*.

- EE. Occasionally spinescent, young branches 0.5 mm. thick, grayish-green; stipules mostly more than 1 mm. long. Washington, Oregon, Idaho, occasionally California.4. *F. stipulifera*.
- DD. Stipules less than 0.5 mm. long, without glandular base.
- E. Young branches grayish-yellow; petals somewhat constricted below the apex. Eastern Utah to northern Colorado.5. *F. meionandra*.
- EE. Young branches grayish-green; petals not so constricted. Oklahoma and Panhandle Plains of Texas.6. *F. planitierum*.
- CC. Stipules absent.
- D. Strongly spinescent; leaves lanceolate to oblanceolate; petals very narrowly oblanceolate, 5-8 mm. long, 0.4-0.8 mm. wide. New Mexico to El Paso region of Texas.7. *F. spinescens*.
- DD. Not spinescent; leaves very broadly oblanceolate; petals lanceolate, 5-7 mm. long, 1.5 mm. wide. Uvalde County, Texas.8. *F. texensis*.

Treatment of Species

1. FORSELLESIA PUNGENS (Brandg.) Heller, Cat. N. Am. Pl., ed. II, 130, 1900.

Glossopetalon pungens Brandegee, Bot. Gaz. 27:445. 1898.

Low diffusely branched, apparently matted, not spinescent, 5-20 cm. high, 30-60 cm. in diameter; young branches slender, scarcely 1 mm. thick, pubescent or glabrous, somewhat ribbed; leaves narrowly elliptical, acute at both ends, ending in a spine 1 mm. long, crowded, unusually thick especially along the margins and veins, scabrous-pubescent or glabrous, 6-10 mm. long, 2-3 mm. wide; without stipules; flowers terminal on short branches; pedicels 3-4 mm. long with 3 or 4 scarious bracts at the base; sepals 5, ovate, acuminate, 2 or 3 of them spinose-tipped, denticulate, hyaline-margined; petals 5, broadly oblanceolate, 6-8 mm. long, 2 mm. wide; stamens 10, the 5 opposite the petals as long as the sepals and the 5 opposite the sepals one-third longer; carpels 1-3, slightly pubescent, ovoid, less than 1 mm. long, 1-(2-) ovuled.

KEY TO VARIETIES

- Leaves and stems scabrous-pubescent.1a. *F. pungens* var. *typica*.
Leaves and stems glabrous.1b. *F. pungens* var. *glabra*.

- 1a. *Forsellesia pungens* (Brandg.) Heller var. *typica* n. nom.

Leaves and stems scabrous pubescent. Growing on rocks at 4000-5000 ft. elevation. Sheep Mountains, Clark Co., Nevada, *Purpus* 6131 in 1898, type collection (UC, US). (See Fig. 1.)

- 1b. *Forsellesia pungens* (Brandg.) Heller var. *glabra* n. var.

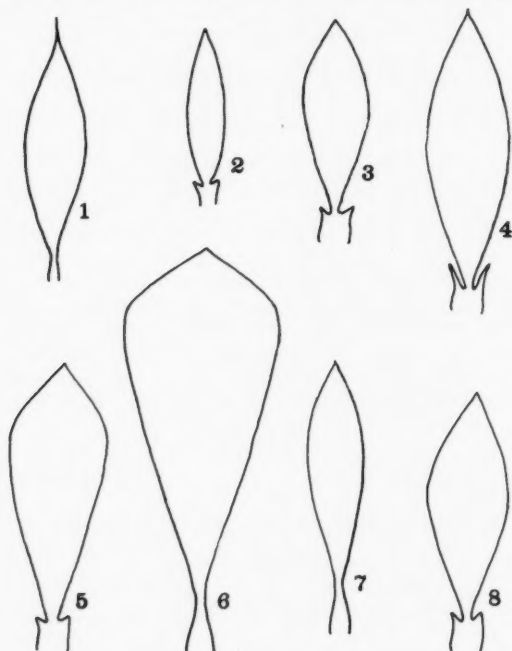
Leaves and stems glabrous. Caules foliaque glabra.

Type from Clark Mountains, eastern Mohave Desert, San Bernardino County, California, *E. C. Jaeger*, June 22, 1930, Pomona College Herbarium number 180226. Other collections from Mohave Desert, 1 mile south of Coliseum Mine, *Wolf* 7066 (RSA), 9582 (RSA).

This species is so distinct from the others that there has been some doubt as to whether or not it really belongs to the genus *Forsellesia*. The habit of growth is quite different from the others in that it is a very low matted shrub. The plants are not spinescent, but some of the other species are not very spinescent. The stems are not smooth as in some of the other species, but are covered with a scaly material probably caused by the crowded leaves. The most distinctive features of the plant are the spine-tipped leaves which no other species have and the terminal inflorescence instead of the usually axillary type.

2. *Forsellesia* Clokeyi n. sp.

Low intricately branched, weakly spinescent, 15-20 cm. high, 30-45 cm. in diameter; young branches very fine, scarcely 0.5 mm. thick, slightly pubes-



Figs. 1-8. Leaves of the species of *Forsellesia*. 1. *F. pungens*, drawn from Purpus 6131, leaf 8 mm. long. 2. *F. Clokeyi*, drawn from Clokey 8667, leaf 5 mm. long. 3. *F. nevadensis*, drawn from Munz 12982, leaf 7 mm. long. 4. *F. stipulifera*, drawn from Henderson 4855, leaf 9 mm. long. 5. *F. meionandra*, drawn from Rollins 1986, leaf 6 mm. long. 6. *F. texensis*, drawn from Palmer 12331, leaf 12 mm. long. 7. *F. spinescens*, drawn from Hansen 391, leaf 8 mm. long. 8. *F. planitierum*, drawn from Stevens 463, leaf 8 mm. long.

cent, characteristically ribbed; leaves oblong-oblancoale, acuminate, slightly pubescent, 5-6 mm. long, 1-1.5 mm. wide; stipules lance-deltoid, less than 0.5 mm. long with bases neither swollen nor glandular; flowers axillary; pedicels with 3 or 4 reduced scarious bracts at the base; flower parts reduced in number; sepals 3-5, unequal, obovate, acute to obtusish, entire and hyaline-margined, 1.2-1.5 mm. long; petals 3-5, oblanceolate, 3 mm. long; stamens 4-6, of equal length; carpel 1, ovoid, scarcely 1 mm. long; mature fruit broadly ovoid, somewhat striated, 3-4 mm. long and 2 mm. wide. (See Fig. 2.)

Planta humilis tortuose ramosa, spinescens, 15-20 cm. alta, 30-45 cm. lata; ramis tenuibus, 0.5 mm. crassis, viridibus, subpubescentibus; foliis oblongo-oblancoale, acuminatis, subpubescentibus, 5-6 mm. longis, 1-1.5 mm. latis; stipulis lanceolato-deltoidis, vix 0.5 mm. longis, basibus non dilatatis; numero partium floris reducto; sepalis 3-5, inaequalibus, obovatis, acutis aut obtusis, 1.2-1.5 mm. longis; petalis 3-5, oblanceolatis, 3 mm. longis; staminibus 4-6; folliculis solitariis, ovoideis, 3-4 mm. longis, 2 mm. latis.

Growing on limestone and in rock crevices at 8000 ft. elevation, Kyle Canyon, Charleston Mountains, Clark Co., Nevada, *Clokey* 8667, June 12, 1940 (type *Clokey* herbarium, isotype Pom). A second collection is from the same place, *Alexander* 751, June 10, 1939 (UC). This species has been named for Mr. I. W. *Clokey* who has devoted much time in recent years to working up the botany of the Charleston Mountains.

This new species is strikingly different in appearance from *F. nevadensis* to which it is closest in relationship. It is quite distinct from the others in the reduced size as well as number of floral parts. To begin with, it is a very much smaller shrub not only in height and diameter but also in the thickness of the branches and leaves. The stipules show a closer relationship to those of *F. nevadensis* than to any of the other species. However, they are reduced to small lance-deltoid projections less than 0.5 mm. long. Even the flower parts are reduced, including the number of stamens and carpels as well as the number of sepals and petals. *F. nevadensis* shows a little reduction; for occasionally the flowers are 4-merous. *F. Clokeyi* goes even further than this with 3-merous in addition to 4- and 5-merous flowers. The number of stamens may be as low as 4; however, unlike *F. nevadensis*, *F. Clokeyi* has its stamens equal in length. As yet only two collections of *F. Clokeyi* have been made and from one locality, but it is so unlike the other species in its reduction that I feel quite justified in describing it as a new species.

3. FORSELLESIA NEVADENSIS (Gray) Greene, *Erythea* 1:206. 1893.

Glossopetalon nevadense Gray, *Proc. Am. Acad.* 11:73. 1876.

Freely or intricately, divaricately branched, spinescent, 1 dm.-18 dm. high; stems ribbed, pubescent or glabrous, young branches more than 1 mm. thick, becoming yellowish as they get older; leaves scattered along the stem or crowded in fascicles, grayish-green to brighter green, oblong to oblanceolate, acuminate to abruptly tipped, 5-12 mm. long, 2-4 mm. wide; petioles 1 mm.

long; stipules subulate, less than 1 mm. long, adnate to a persistent often thickened glandular base, usually not present in fascicled leaves; flowers axillary, 4-5 merous; pedicels 3-5 mm. long with several reduced leaves or scarious bracts; sepals entire, hyaline margined, ovate, 1-3 mm. long; petals oblanceolate, 4-7 mm. long; stamens 6-10, unequal, the longer stamens opposite the sepals and about one-third longer; carpels 1-2; mature fruit striated, ovoid, 5 mm. long.

KEY TO FORMS

- Leaves and stems pubescent 3a. *F. nevadensis* f. *typica*.
 Leaves and stems glabrous 3b. *F. nevadensis* f. *glabra*.

3a. *Forsellesia nevadensis* (Gray) Greene forma *typica* n. nom.

Forsellesia arida (Jones) Heller, Cat. N. Am. Pl. ed. II, 130. 1900.

Glossopetalon spinescens var. *aridum* Jones, Cont. Bot. 8:28. 1898.

Glossopetalon nevadense Gray, Proc. Am. Acad. 11:73. 1876.

Leaves and stems pubescent.

Type locality, "Northern part of Washoe County, Nevada." Growing at 3500-7000 ft. elevation in Nevada, northern Arizona, and eastern California.

Specimens seen: NEVADA: Washoe Co., Pyramid Lake, Lemmon in 1875 (type GH); West shore of Pyramid Lake, Lemmon, June 1875, 1879 (UC, US); Laughton Springs below Verdi, Sonne, May and June 1890 (Pom, US) and May 1897 (Pom, UC, US); Elko Co., Ferguson Springs, Jones, June 1900 (Pom); Storey Co., Virginia City, Hooker and Gray in 1877 (GH); Mineral Co., Hawthorne, Lepantha Mines, Jones in 1897 (type collection *F. arida* Pom, US); Clark Co., Mountain Spring, Charleston Mts., Coville and Funston 1880 (US).—ARIZONA: without definite locality, Palmer 611, in 1869 (US); Mohave Co., Peach Spring, Lemmon (UC); Rocky Wash below Black Rock Spring, Jones 5097, (Pom, UC); Coconino Co., Grand Canyon. Lemmon in 1884, (UC, US); Diamond Creek Canyon, Wilson in 1893 (UC).—CALIFORNIA: Inyo Co., Tin Mountain, Death Valley, Gilman 2389 (Pom); Grapevine Mts., Death Valley, Eastwood, and Howell 7798 (CAS); Titus Canyon, Death Valley, Munz 16461 (CAS, GH, Pom, UC, US) and Howell in 1940 (Pom); San Bernardino Mts., S. B. and W. F. Parish 1291, (DS, GH); Cushenbury Grade, Munz 13936 (DS, Pom, UC) and Newsom and Hilend in 1927, (Pom).

3b. *Forsellesia nevadensis* (Gray) Greene forma *glabra* n. forma.

Leaves and stems glabrous with an occasional slight short stiff pubescence on the leaf margins. Folia caulesque glabri aut subglabri. (See Fig. 3.)

Type, New York Mountains, eastern Mohave Desert, San Bernardino Co., California, Munz 13739, May 4, 1935 (Pom), isotypes at Stanford and University of California. Range from Idaho and western Utah to Grand Canyon, Arizona, and west to Mohave Desert.

Material seen: IDAHO: near Whitebird, Salmon River, Bailey 50, (US). UTAH: without locality, Parry 27, (GH, Pom, US); Millard Co., Preuss Lake, Tidestrom 11153, (US); Washington Co., St. George, Parry, in 1874, (GH); southern Utah and northern Arizona, Palmer 75, in 1877 (GH).—NEVADA: Washoe Co., Spanish Spring, northeast of Reno, Hendrix 852, (UC, USDA); Truckee Pass, Heller 9594, (DS, GH, US), Kennedy 2026 (DS); Lander Co., Tobe Rogers ranch, Smokey

Valley 50 mi. so. of Austin, *Murphey* 4752 (USDA); Storey Co., North east of Virginia City, *Adams* 163, (UC); White Pine Co., Mount Moriah, head of Nigger Creek, *Train* 1189 (USDA); Muncy, *Jones* in 1906 (DS, Pom, US); Esmeralda Co., without definite locality, *Shockley* 588 (UC); Lincoln Co., 2 miles above Adam Springs on road to summit of Mt. Irish, *Train* 2404 (USDA); Pahroc Spring, *Bailey, Coville, and Funston* in 1891, 1896 (US).—ARIZONA: Mohave Co., Hualpai Indian Reservation, *Plumb* in 1936 (US); Peach Spring, *Wilson* in 1893 (UC, US); Hackberry, *Jones* 4404 (US); Coconino Co., south end of Navajo Mt., *Peebles* 13925 (UC); Bright Angel Trail, Grand Canyon, *Goldman* 2072 (US) and *Mrs. Meiore* in 1917 (CAS); Hermit Trail, Grand Canyon, *Eastwood* 5952 (CAS, GH); Grand View Trail, Grand Canyon, *Eastwood* 5751 (CAS), 3587 (CAS) and *Ferris* and *Duncan* 2260 (CAS, DS).—CALIFORNIA: Inyo Co., White Mts., *Purpus* 5794 (Pom, UC, US); Mt. Laura, *Purpus* 5520 (GH, UC, US); Panamint Mts., above Surprise Canyon, *Howell* 3950 (CAS, UC); San Bernardino Co., Clark Mts., *Munz* 12882 (Pom, UC) and 12982 (Pom, US); New York Mts., east Mohave Desert *Wolf* 9646 (RAS).

Forsellesia nevadensis and *F. spinescens* have long been confused, and *F. nevadensis* has often not been recognized as distinct. The characters which were formerly used to differentiate these species were vague and inaccurate. A definite differentiation can be obtained by use of the stipules which are lacking in *F. spinescens* and persistent and adnate to a thickened leafbase in *F. nevadensis*, remaining on the stem even after the leaves are shed. Gray, 1. c., described *F. nevadensis* as having 4-merous flowers but I find that 5-merous flowers are more frequent in this species.

4. *Forsellesia stipulifera* (St. John) n. comb.

Glossopetalon stipuliferum St. John, Fl. S. E. Wash. and adj. Idaho, 250. 1937.

Freely branched, glabrous, 1-3 meters high, occasionally spinescent; young branches 0.5 mm. thick; leaves glabrous, not crowded, grayish green, oblanceolate, acute, 6-17 mm. long, 2-3 mm. wide, from a dark swollen glandular base; petioles 1 mm. long; stipules 0.5-1 mm. long, lanceolate to subulate; flowers axillary, 5-merous; pedicels 2-5 mm. long with several scarious bracts at the base; sepals entire, hyaline-margined, lanceolate-ovate, 2 mm. long, little more than 1 mm. wide; petals linear-oblanceolate, 6-9 mm. long, 1 to almost 3 mm. broad; stamens 5-8, equal; carpels solitary, 3-5 mm. long, slightly more than 2 mm. wide, asymmetrically ovoid, acute, 1 mm. long. (See Fig. 4.)

Type locality, Snake and Clearwater Rivers near Lewiston, Idaho. The type *Henderson* 4855, is in the Herbarium of State College of Washington. Growing on limestone from 2000-5500 ft. and ranging from Washington and Idaho to California. Specimens seen: WASHINGTON: without locality *Sheldon* in 1897 (US).—OREGON: Wallowa Co., Snake River Canyon near Mouth of Battle Creek, *Peck* 18167 (CAS); Malheur Co., Bluffs of Snake River, *Cusick* 916 (GH, US); Cliffs of MacDougal Creek near Snake River, *Cusick* 2534 (GH, Pom, UC, US); Leslie Gulch near Owyhee River, *Henderson* 8066 (CAS, UC).—CALIFORNIA: Trinity Co., Trinity River Canyon near Eagle Creek, *Howell* 12839 (CAS); Inyo Co., Black Canyon, White Mts., *Duran* 548 (DS, Pom, RAS, UC, US). IDAHO: Nez Perce Co., Snake and Clear River Canyons near Lewiston, *Henderson* 4855, isotypes (GH, DS, US); mouth of Salmon River, *Eastwood* 13331 (CAS).

Forsellesia stipulifera may be distinguished from *F. nevadensis* to which

it is closely related by its longer stipules and its more northern range. Its range overlaps slightly in the White Mountains; for the White Mountains are the southernmost limit of many northern species of plants. It is not nearly as spinescent as *F. nevadensis*, but its stipules are also adnate to a persistent often glandular base.

A specimen of Jones in July 1909 (Pom) from Alta, Montana, is so unusual that it deserves special notice. Instead of the usual tall, freely branched shrubs, this one is low, with recurved, closely and intricately branched stems. The leaves are much smaller, 1-5 mm. long, 1-1.5 mm. wide. Since the flowers are past anthesis, there are very few petals remaining, those seen being slightly more than 1 mm. long. It is only because the stipules are not reduced in size and the leaves are of the same general shape that it is not considered to be a distinct species. Should more specimens be collected with the smaller petals and the recurved branches, it might well be described as a new species.

5. *FORSELLESIA MEIONANDRA* (Koehne) Heller, Cat. N. Am. Pl., ed. II, 130, 1900.

Glossopetalon meionandrum, Koehne, Gartenflora 43:237, fig. 52, 1894.

Low, spinescent, leafy, not much over 6 dm. high; young branches grayish yellow, about 1 mm. thick, older branches gray with splitting bark; leaves oblanceolate, gray-green, pubescent, acute, 7-15 mm. long, 3-4 mm. broad; petioles 1 mm. long; stipules subulate, less than 0.5 mm. long; flowers axillary; pedicels with scarious bracts at the base; sepals 5, 3 mm. long, 2 mm. wide; disc more or less cup-shaped; petals 5, oblanceolate, somewhat constricted below the apex, 4-6 mm. long, slightly more than 1 mm. broad; stamens 5-7; carpel 1, less than 1 mm. long; follicles 4 mm. long, 3 mm. wide (See Fig. 5).

Type locality: North bank of Surface Creek, Mesa Grande, Delta Co., Colorado at 6000 ft. Purpus 71, May 1892. Ranging from eastern Utah to northern Colorado. Specimens seen: UTAH: San Pete Co: Gunnison. Jones in 1911 (Pom), and in 1910 (Pom); South of Sterling, Tidestrom 2090 (US); Anderson Co. 7 mi. northwest of Ephraim, Eggleston 10138 (USDA); Duchesne Co., 10 mi. west of Duchesne, Stoddard and Passey in 1936 (Pom); Carbon Co., head of Soldier Canyon, Jones 5590a (US); Emery Co., Orangeville, Jones in 1894 (Pom); Spring Glen, Jones in 1896 (DS. Pom. UC, US); Daggett Co.: Flaming Forge, 15 mi. southeast of Manila, Rollins 2273 (Pom); Uintah Co., Fort Duchesne, Duchesne Valley, Jones in 1908 (Pom); Theodore, benches of the Uintahs, Jones in 1908 (Pom); San Juan Co., White and Armstrong Canyons, near Natural Bridges, Rydberg and Garrett 9403 (US).—COLORADO: without locality, Flowers 41-30 in 1930 (DS), and Clear Creek Canyon, Jones 6106a (Pom, US) and 5590a (Pom); Mesa Co., Grand Junction, Eastwood in 1891 (UC); Montrose Co., Bostwick Park, near Montrose, Payson 677 (GH); Delta Co., 8 mi. west of Delta near Gunnison River, Rollins 1986 (GH).

Forsellesia meionandra may be separated from all of the other species by its distinctive petals which are slightly constricted below the apex. While I have not seen the type specimens I have seen the drawings made from them. It is apparent, after studying the group, that the drawings exaggerate the constriction. The shrubs are much leafier than the others.

6. *Forsellesia planitierum* n. sp.

Intricately branched, spinescent; young branches less than 1 mm. thick; leaves lanceolate, pubescent, (veins thickened and prominent on the under side), 6-12 mm. long, 2.5-4 mm. wide; petioles less than 1 mm. long; stipules subulate, less than 0.5 mm. long; flowers axillary; pedicels 1-3 mm. long with scarious bracts at the base; sepals 5, ovate, 1.5-2 mm. long, 1 mm. wide; petals 5, oblanceolate, 4-6 mm. long, 1.5-2 mm. wide; stamens 8, unequal in length; carpels solitary, less than 1 mm. long; mature follicles ovoid, 4-5 mm. long. (See Fig. 8.)

Planta tortuose ramosa, spinescens; ramis parvis vix 1 mm. crassis, caulibus pubescentibus; foliis lanceolatis, pubescentibus, 6-12 mm. longis, 2.5-4 mm. latis; petiolis vix 1 mm. longis; stipulis subulatis, usque 0.5 mm. longis, pedicellis 1-3 mm. longis; sepalis 5, ovatis, 1.5 mm. longis, 1 mm. latis; petalis 5, oblanceolatis, 4-6 mm. longis, 1.5-2 mm. latis; folliculis solitariis, ovoideis, 4-5 mm. longis.

Type, Black Mesa, near Kenten, Cimarron Co., Oklahoma, *Stevens* 463 (GH, isotypes US and DS). Range, Panhandle region of Texas and Oklahoma.

Specimens seen: without locality, Llano Estacado, *Bigelow* in 1853-54 (US).—OKLAHOMA: Cimarron Co., Black Mesa, *Ortenburger* in 1926 (US).—TEXAS: Randall Co., Canyon, *Benke* 4984 (US); Armstrong Co., Gamble's Ranch, *Palmer* 13954 in 1918 (US); Lubbock Co., Johnson's Ranch, *Reed* 5971a (US); Marion Co., Caddo Lake Region, *Hams* 470 (US).

Since I have not seen this species growing, it is difficult to tell from the specimens much about the size of the shrubs. It seems to be a distinct species with a definite geographical range. It may be distinguished from *F. nevadensis* by its grayer and thinner stems and leaves. It is not nearly so spinescent as *F. nevadensis* and *F. spinescens*. Its petals are much broader than those of any of the other species. Geographically Dr. Hams' specimen collected from the Caddo Lake region does not belong to this group; for this is near the Louisiana border and the conditions under which it grows are probably much different from those of the Panhandle Plains. Until more collections have been made from this region, it seems best to leave it in this group. Judging from the single collection it agrees fairly well in its morphological characters.

7. *FORSELLESIA SPINESCENS* (Gray) Greene, *Erythea* 1:206. 1893.

Glossopetalon spinescens Gray, *Pl. Wright*. 2:29. pl. 12. 1853.

Intricately branched, very spinescent, 3-9 dm. high; young branches slightly less than 1 mm. thick; leaves lanceolate to oblanceolate, glaucous, very acute, 5-11 mm. long, 1-2.5 mm. wide; stipules absent; petioles 2 mm. long; flowers axillary, pedicels 1-5 mm. long with scarious bracts at the base; sepals usually 5, lanceolate to oblanceolate, 5-8 mm. long, 0.4-0.8 mm. broad; stamens 6-10, equal or unequal; follicles broadly ovoid.

KEY TO VARIETIES

- Leaves 5-11 mm. long, 1-2.5 mm. wide; pedicels 4-5 mm. long; sepals equal; petals oblanceolate, 8 mm. long; stamens 6-10, equal.7a. *F. spinescens* var. *typica*.
 Leaves 5-7 mm. long 1-1.5 mm. wide; pedicels 1-3 mm. long; sepals unequal; petals lanceolate, 5 mm. long; stamens 7-8, unequal.7b. *F. spinescens* var. *mexicana*.

7a. *Forsellesia spinescens* (Gray) Greene var. *typica* n. nom.

Glossopetalon spinescens Gray, Pl. Wright. 2:29, 1853.

Leaves lanceolate to oblanceolate, 5-11 mm. long, 1-2.5 mm. wide; pedicels 4-5 mm. long; sepals equal; petals oblanceolate, 8 mm. long; stamens 6-10, equal. (See Fig. 7.)

Type, Mountain Ravine near Frontera, New Mexico, Wright 1347 in April 1852 (GH). Range: New Mexico, Arizona to El Paso region of Texas.

Material seen: NEW MEXICO: Dona Ana Co., Summit of Organ Mts., Lemmon 122 (GH), and in 1881 (Pom, UC); Bishops Gap, Organ Mts., Woolon, in 1903 (US); Guadalupe Mts., near Sitting Bull Falls, Standley 40751 (US); Grant Co., Upper Corner Monument, Mearns 63 (DS, US); San Andreas Mts., Sheep Mt., Gout 34 (US); Brewster Co., Marathon, Hansen 391 (GH, US).—TEXAS: Fort Bliss, Mrs. Clemens in 1917 (CAS); El Paso Co., El Paso, Thurber 159 (GH), and Jones 3724 (US); Franklin Mts., near El Paso, Barlow in 1911 (US).—ARIZONA: without definite locality, Palmer 611, in 1869 (US); Mustang Mts., Pringle in 1884 (GH); Chiricahua Mts., Lemmon in 1881 (UC); Mexican Boundary Survey, Parry, Bigelow, Wright, Schott (US).

Forsellesia spinescens is generally a much smaller shrub than *F. nevadensis*. It is further differentiated from *F. nevadensis* by its absence of stipules and its longer and narrower petals.

7b. *Forsellesia spinescens* (Gray) Greene var. *mexicana* n. var.

Leaves oblanceolate, 5-7 mm. long, 1.5 mm. wide; pedicels 1-3 mm. long; sepals unequal; petals lanceolate, 5 mm. long; stamens 7-8, unequal. (Folia 5-7 mm. longa, 1.5 mm. lata; pedicellis 1-3 mm. longis; sepalis inaequalibus; petalis lanceolatis, 5 mm. longis; staminibus 7-8, inaequalibus).

Type, Sierra Pata Galana, Coahuila, Mexico, Purpus 1120 in Feb. 1905. (UC). *Forsellesia spinescens* var. *mexicana* in many respects is so different from *F. spinescens typica* that it perhaps should be treated as a species. Since there is, however, only one collection of it and it does have points in common with *F. spinescens typica*, such as absence of stipules and the general type of growth, it seems wise to keep it as a variety, until further collections may become available.

8. *Forsellesia texensis* n. sp.

Tall, closely branched, spinescent; young branches 1 mm. in diameter, glabrous; older branches dark gray; leaves very broadly oblanceolate, acute to mucronate, frequently with margins and veins thickened, generally glabrous with occasional pubescence, 1-2 cm. long, 3-5 mm. wide; stipules absent; petioles

1 mm. long; flowers axillary; pedicels 5 mm. long with 4-5 scarious bracts at the base; sepals 5, entire, hyaline-margined, ovate, 2 mm. wide; stamens 7-9, equal; carpels solitary, mature follicle very broadly ovoid, 4-5 mm. long. (See Fig. 6.)

Planta alta, spinescens, ramis parvis, 1 mm. crassis, glabris; ramis majoribus fumosis; foliis late oblanceolatis, 1-2 cm. longis, 4-5 mm. latis, acutis ad mucronatis, marginibus et venis incrassatis, glabris; stipulis nullis; sepalis 5, ovatis, 2 mm. longis; petalis 5, lanceolatis, 5-7 mm. longis, 1.5 mm. latis; staminibus 7-9, aequalibus; folliculis solitariis, ovoideis, 4-5 mm. longis.

Type, Montell, Uvalde Co., Texas, *Palmer 12331*, June 1917 (CAS, isotype UC), growing on limestone, Uvalde Co., Texas.

Specimens seen: TEXAS: Uvalde Co., *Palmer 12980 in 1917* (CAS, UC); Nueces River, "Chalk Bluff," *Palmer 13345*; in 1918 (US, CAS).

This new species has such broad oblanceolate leaves with thickened margins that it is easily distinguishable from the other species. Because of its absence of stipules it is probably closest to *F. spinescens* in relationship.

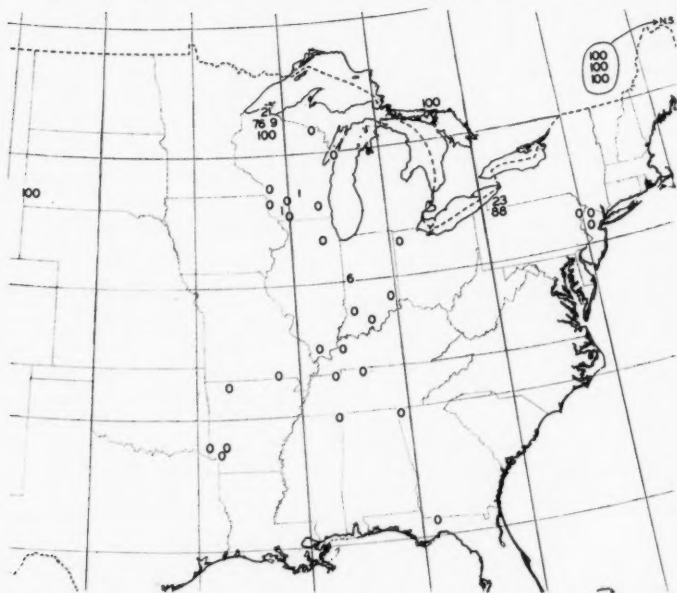
POMONA COLLEGE,
CLAREMONT, CALIFORNIA.

Mass Collections: *Ranunculus abortivus* and Its Close Relatives

Norman C. Fassett

These species vary in the pubescence of the stem and peduncles, and in the shape of the basal leaves. Mass collections have therefore been made consisting of a characteristic basal leaf and portion of the inflorescence of each plant. These were usually supplemented by a few entire plants.

RANUNCULUS ABORTIVUS L., var. *ACROLASIUS* Fernald, *Rhodora* 40:418. 1938, with the stem and young peduncles minutely pilose, is designated as the northern phase of the species, ranging south to Maine, Massachusetts, northern Rhode Island and Connecticut, western New York, northern Michigan, South Dakota, Wyoming, and in the Rocky Mountains to Colorado. Its range overlaps that of the more southern, glabrous, var. *typicus*, which



Map 1. *R. abortivus*. Percentage of individuals in each collection having pilose stems (var. *acrolasius*).

nation of authentic material in the Gray Herbarium and the Herbarium of the New England Botanical Club shows specimens from within the range of var. *acrolasius* to be pilose like that variety, and those from within the range of var. *typicus* to be glabrous like that variety. There is in the New York Botanical Garden a perfectly characteristic sheet of var. *eucyclus* from Devils Lake, North Dakota. Mass collections contain var. *eucyclus*, not only within the range ascribed to it, but also from Ohio (Fig. 1), Indiana (Fig. 2), Illinois and Wisconsin. The figures on Map 2 indicate the percentage of var. *eucyclus* in collections from each region. Except in the southern states, it occurs sporadically within the range of var. *typicus* and var. *acrolasius* alike, always

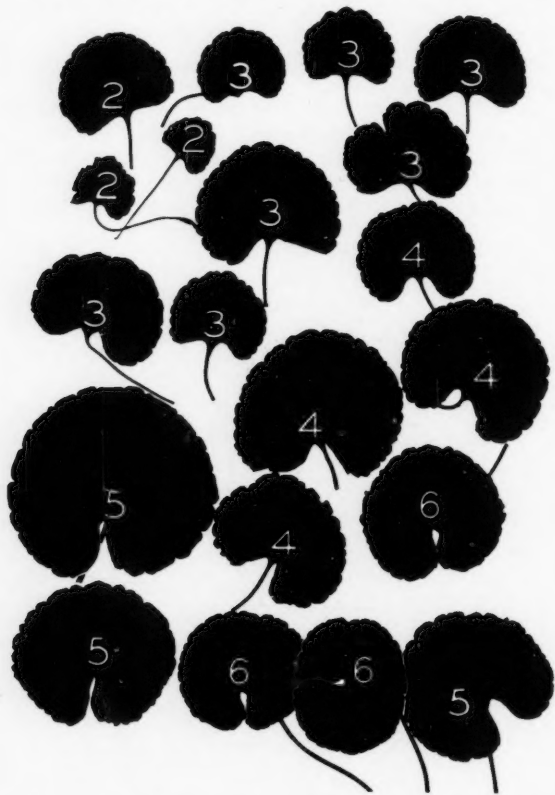


Fig. 1. *R. abortivus*. Basal unleft leaves of Collection 29 from Napoleon, Ohio. $\times 1/2$. The three overlapping leaves in the lowest row are on one plant.

The number on each leaf indicates the leaf type as listed in Table 1.

in company with a majority of individuals whose basal leaves are merely cordate or truncate.

In absence of strong geographic or other segregation, var. *eucyclus* seems not worthy of recognition even as a form (in fact there would have to be two forms, one of var. *typicus* and one of var. *acrolasius*). The fact is simply that the basal leaves vary from cuneate to deeply cordate at base, as is shown in Figs. 1-3. They almost always vary on the same plant, as is shown in Fig. 4. In the north they range from cordate to very deeply cordate, and vary only slightly in the other direction to truncate or cuneate (Figs. 1 & 2). In the south they range from cordate to truncate and sometimes cuneate (Fig. 3). These tendencies are expressed numerically in Table 1, where six types of leaves are recognized, ranging from cuneate to deeply cordate with overlapping lobes. Type 1 is cuneate at base; 2 is truncate; 3 is cordate with the angle of the sinus more than 90 degrees; 4 is more deeply cordate with the angle of the sinus less than 90 degrees, often with parallel sides, but wider than deep; 5 has a sinus deeper than wide; 6 has the basal lobes overlapping. Numbers on the leaves in most of the figures indicate the type. Types 5 and 6 embrace var. *eucyclus*, described as having a narrow or nearly closed sinus, and illustrated by its author with a closed sinus (*Rhodora* 40: Plate 519, fig. 3. 1938).

By assigning an arbitrary value to each type, a figure may be obtained

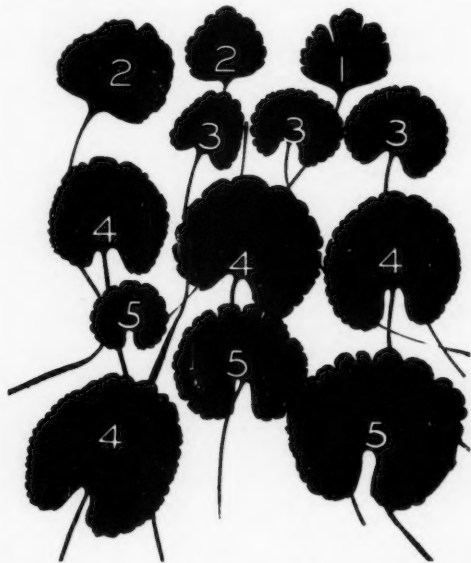


Fig. 2. *R. abortivus*. Basal unclift leaves of Collection 30 from Veedersburg, Indiana, $\times 1/2$.

TABLE I.—*R. abortivus*.

	Stem, etc. glab-pubes- cent	leaf types						Av.
		1	2	3	4	5	6	
1. NOVA SCOTIA: Five Is., Cumberland Co.	0 10	0	0	5	1	1	1	38
2. East Napleton	0 11	0	1	3	2	1	0	34
3. Near Truro	0 5	0	0	3	2	0	0	
4. Near Truro	0 8	0	4	4	0	0	0	
5. Near Truro	0 6	0	0	1	2	1	1	
Total Truro collections	0 19	0	4	8	4	1	1	33
6. ONTARIO: 10 miles west of Warren	0 9	0	0	12	5	8	1	39
7. WISCONSIN: near Ashland	27 7	3	6	6	11	0	0	30
8. Between Ashland and Odanah	5 16	0	4	4	4	1	0	32
9. Bear Trap, near Ashland	31 3	1	3	24	5	0	0	30
10. Bad River Falls, near Ashland	0 10	0	0	1	5	2	0	41
11. Eagle River	0	1	36	16	0	0	33
12. Crandon	11 0	0	0	6	3	1	0	35
13. Sturgeon Bay	10 0	0	0	2	9	5	0	42
14. Humbird	0	0	18	2	0	0	31
15. Coon Valley	20 0	0	0	11	5	3	3	39
16. Poynette	104 1	0	3	66	33	5	0	34
17. Jefferson	10 0	0	1	3	4	2	1	39
18. Clyde	20 0	0	1	14	13	0	0	34
19. Wyalusing State Park	13 0	0	0	10	6	0	0	34
20. Platteville	68 1	0	6	27	24	1	0	33
21. Big Patch	67 0	0	1	40	25	3	0	34
22. SOUTH DAKOTA: Keystone, Black Hills	0 10	0	3	7	1	0	0	28
23. Sylvan Lake, Black Hills	0 30	1	11	15	1	0	0	26
24. NEW YORK:								
Bear Cave Trail, Allegany State Park	40 12	0	1	15	19	18	2	41
25. France Brook, Allegany State Park	2 14	0	0	2	4	2	0	40
26. NEW JERSEY: Newton	25 0	0	0	15	8	0	0	33
27. Somerville	26 0	0	4	23	2	0	0	29
28. PENNSYLVANIA: Matamoras	9 0	0	1	16	17	4	0	36
29. OHIO: Napoleon	28 0	0	3	16	16	5	3	37
30. INDIANA: Veedersburg	13 0	1	2	2	7	1	0	
31. Veedersburg	4 1	0	0	0	1	3	1	
Total Veedersburg collections	17 1	1	2	2	8	4	1	38
32. Brazil	23 0	0	4	14	9	1	0	
33. Brazil	10 0	0	1	6	2	3	0	
Total Brazil collections	33 0	0	5	20	11	4	0	34
34. Derbyshire Falls	37 0	0	1	15	19	7	0	38
35. Oolitic	3 0	0	0	1	2	1	0	
36. Oolitic	7 0	0	1	3	2	0	0	
Total Oolitic	10 0	0	1	4	4	1	0	35
37. ILLINOIS: Elburn	12 0	0	0	3	9	1	0	38
38. Giant City State Park	28 0	0	3	11	20	3	0	36
39. Giant City State Park	10 0	0	0	5	4	1	0	36
40. KENTUCKY: Madisonville	26 0	0	3	22	2	0	0	30
41. TENNESSEE: South of Fulton, Kentucky	38 0	5	7	15	5	0	0	26
42. Pleasant View	18 0	0	1	14	3	1	0	37
43. MISSOURI: West Plains	12 0	0	2	4	4	0	0	32
44. GEORGIA: Chicamauga Battlefield	14 0	0	0	10	0	0	0	30
45. MISSISSIPPI: Corinth	47 0	1	9	29	5	0	0	29
46. ARKANSAS: Ponca	10 0	0	7	5	0	0	0	24
47. Boxley	29 0	1	10	17	1	0	0	26
48. Bog Springs	19 0	0	3	14	1	0	0	29

TABLE 1.—*R. abortivus* (Continued)

Av.		Stem, etc. glab- pubes- rous cent	leaf types						Av.
			1	2	3	4	5	6	
38	49. White Cliff	11	0	1	7	6	0	0	24
34	50. Hope	24	0	6	12	8	0	0	21
	51. FLORIDA: Tallahassee	7	0	0	2	3	2	0	30

representing the average leaf base of each collection. The average is determined as follows: the number of individuals in type 1 is multiplied by 10, the number of type 2 by 20, and so on up to type 6 whose count is multiplied by 60; the sum of these products is divided by the total number of individuals. It is obvious that a collection composed entirely of type 1 would have an average of 10, a collection of all type 6 would average 60, and a collection with each type represented equally would average 35. Most of the averages in the northern states are in the 30's, because type 3 predominates and there are usually more individuals of the deeply cordate types (types 4-6) than of the cuneate and truncate types (types 1 & 2). In Arkansas, where types 5 & 6 ("var. *euclyclus*") are absent, the tendency away from a deep sinus and

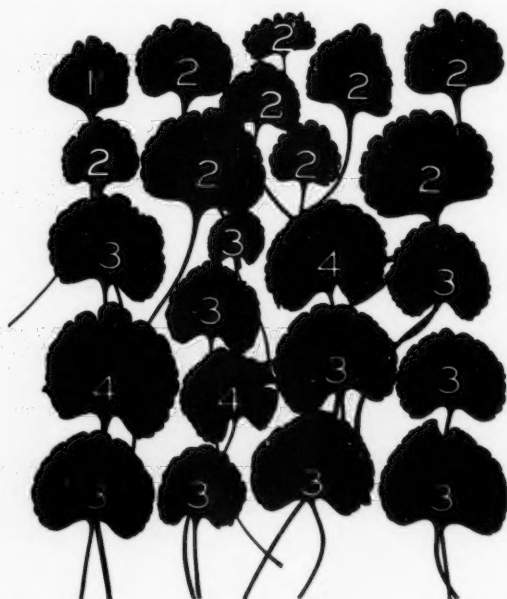


Fig. 3. *R. abortivus*. Basal uncleft leaves of Collection 47 from Boxley, Arkansas. $\times 1/2$.



Fig. 4. *R. abortivus*. An individual of Collection 15 from Coon Valley, Wisconsin, $\times 1/2$.

toward a truncate or cordate leaf is expressed by the lower averages of 21-29.

A glance at Figs. 1-3 gives the impression that the more deeply cordate leaves would average larger than the others. This impression is corroborated by Table 4,¹ which shows the average width of leaves of each type in some of the collections where the more deeply cordate leaves are well represented. Furthermore, on many plants there is a clear correlation of size of leaves and depth of sinus (Fig. 4). So var. *eucyclus* is perhaps at least in part a product of environmental factors, consisting simply of individuals with some of the leaves large and well developed.

¹ In Tables 1-3 only one leaf from each plant was considered. In Table 4 all simple basal leaves on each entire plant represented in the collection were measured as well as the collections of single detached leaves.

R. HARVEYI is represented in collections 52 and 53, Table 2, and by Fig. 5. It is significant that while the averages in this species are the same as those of *R. abortives*, the number of types is smaller. That is, the leaf types of both species center on about the same point, but the spread of variation is much greater in *R. abortivus* than in *R. Harveyi*. This is to be expected, for *R. Harveyi* has a limited range in Missouri, Arkansas and Alabama, while *R. abortivus* is a wide-ranging species.

R. MICRANTHUS (Table 3 and Fig. 6) has a greater tendency toward the cuneate leaf than have the other species, as is indicated by the much lower averages. According to Professor Fernald the *R. micranthus* of the southern states has its basal leaves "usually subcordate to strongly cordate," and the northern plant, distinguished as var. *delitescens* (Greene) Fernald, *Rhodora* 41:543. 1939, has "the simple basal leaves merely subtruncate to cuneate at base." The mass collections from Kentucky and Arkansas certainly have cuneate leaves predominating; a suite of mass collections throughout the range of *R. micranthus* would throw light on the validity of var. *delitescens*, which is described as also differing from the more southern plant in color and toothing of the leaves.

The taxonomic value of a character lies not in how conspicuous it is but in the extent to which it correlates with other characters or with geographic distribution. A character may be "good" in one group and "poor" in another. This is admirably demonstrated by the behavior of pubescence in these three species of *Ranunculus*. Pubescence of stem behaves in three different ways. In

TABLE 2.—*R. Harveyi*.

	Stem, etc.		leaf types						Av.
	glab.	pubes- cent	1	2	3	4	5	6	
52. ARKANSAS: Pettigrew	15	8	0	5	13	0	0	0	27
53. West Fork	50	0	0	2	19	16	0	0	34

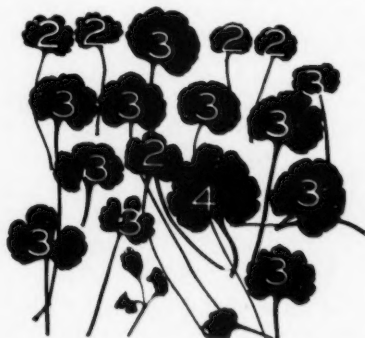
Fig. 5. *R. Harveyi*. Basal leaves of Collection 52 from Pettigrew, Arkansas, $\times 1/2$.

TABLE 3.—*R. micranthus*.

	Stem, etc. glab. pubes- cent	leaf types						6 Av.
		1	2	3	4	5		
54. ILLINOIS: Ramsey	0 39	32	0	0	0	0	0	10
55. KENTUCKY: Otter Creek, near Fort Knox ..		19	1	1	0	0	0	11
56. ARKANSAS: Bee Mt., Mena	0 16	6	9	0	0	0	0	16
57. Shady, near Mena	0 13	10	2	0	0	0	0	12
58. West Fork	0 58	38	20	1	0	0	0	14
59. OKLAHOMA: Tahlequah	0 19	17	0	0	0	0	0	10

TABLE 4.—*R. abortivus*.

Average width, in cm., of each type of basal leaf.

	1	2	3	4	5	6
13. WISCONSIN: Sturgeon Bay			4.2	4.4	4.2	
15. Coon Valley			4.1	4.4	4.1	4.8
16. Poynette		1.4	2.6	3.2	3.0	
24. NEW YORK: Allegany State Park		2.5	2.5	2.9	3.3	3.5
28. PENNSYLVANIA: Matamoras		3.0	3.4	4.0	4.5	
30. & 31. INDIANA: Veedersburg	2.5	3.5	2.9	3.8	4.7	4.0
34. Derbyshire Falls		1.5	2.9	4.1	4.7	
48. ARKANSAS: Boxley		2.5	3.5	3.1	3.0	
Average, these collections	2.5	2.4	3.3	3.7	3.9	4.1

R. micranthus the stem, at least on its lower portion, is always pilose, as far as available material and descriptions indicate; *R. micranthus* has at some time become homozygous for this character. In *R. abortivus* both glabrous and pilose stems occur, but in different parts of the range; it has become homozygous for pilosity in the north and for glabrosity in the south, with an intermediate zone where it is heterozygous. *R. Harveyi* is heterozygous for this character, apparently throughout its range, for pubescent individuals appear sporadically among the glabrous ones. To express these facts in taxonomic terms, we may say that pilosity is a specific characteristic of *R. micranthus*, a varietal characteristic of *R. abortivus* where it sets off var. *acrolasius*, and a formal characteristic in *R. Harveyi* where it is the basis of f. *pilosus* (Benke) Palmer & Steyermark.

Pubescence of petioles is of no taxonomic significance in *R. abortivus*, for petioles may be glabrous, or with a pubescent line, or pubescent throughout, and all these conditions may appear on the same plant.

Pubescence of the receptacle, on the other hand, is of value in separating species. *R. micranthus*, with stems always pubescent, and *R. Harveyi*, with stems often pubescent, are distinguished by their glabrous receptacles from *R. abortivus* which has a pubescent receptacle, but which has glabrous stems in the regions where these three species occur together.

Many of the collections listed in Table 1 were made during travel subsidized by the Wisconsin Alumni Research Foundation. The writer is indebted to Mr. A. E. Roland for Collections 1-5, to Professor Newton T. Bobb for

Collections 7-10, to Mr. L. H. Shinnars for Collections 12, 13 & 59, to Mrs. Margaret Schmidt Bergseng for Collection 20, to Dr. J. W. Thomson, Jr., for Collections 26 & 27, and to Professor Herman Kurz for Collection 51. Maps 1 & 2 are prepared from base maps of Hall's Outline Maps and Graphs, and published by permission of the author and publisher, John Wiley & Sons, Inc. Figs. 1-6 were printed from paper negatives made by direct contact with the leaves; the numbers were inked on the negatives, and the prints touched up to the extent of blocking out holes eaten by insects and indicating the overlapping edges of leaves with a closed sinus.

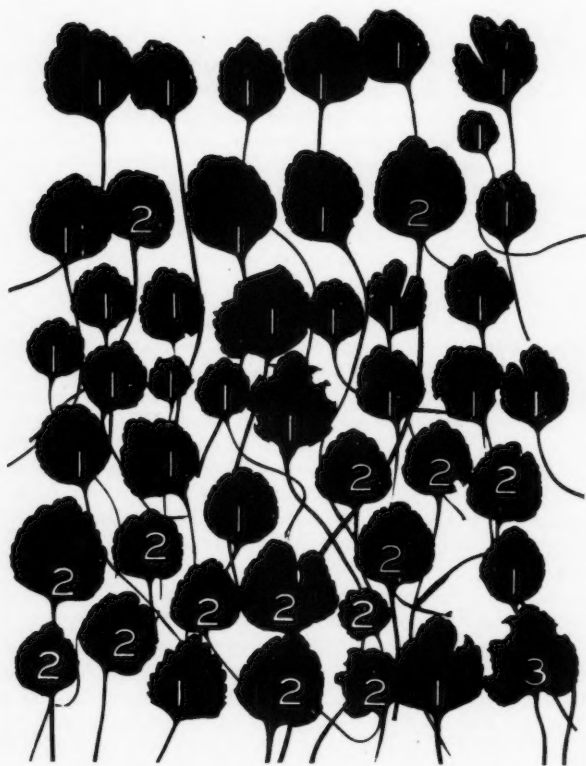


Fig. 6. *R. micranthus*. Basal uncleft leaves of Collection 58 from West Fork, Arkansas, $\times 1/2$.

Summary

The pubescent phase of *Ranunculus abortivus*, segregated as var. *acrolasius* Fernald, is the only representative of that species northward; it occurs with the glabrous phase in Wisconsin, Indiana, New York, and doubtless in other intermediate areas, and is absent from the southern part of the range of the species. Var. *acrolasius* is thus confirmed as a valid geographic variety. Var. *eucyclus* Fernald, with a deep narrow sinus or overlapping basal lobes on the basal leaves, may occur in any colony of *R. abortivus* or its var. *acrolasius*, except in the extreme southern part of the range of the species, and is not a valid geographic variety. To a large degree the type of leaf on which var. *eucyclus* was based represents the best-developed, and usually the largest, leaf on each plant.

The basal leaf of *R. Harveyi* (when not divided) is like the commonest type found in *R. abortivus*, but in *R. Harveyi* there is less tendency toward the extreme leaf-types, i. e., cuneate and deeply cordate. *R. micranthus* shows little variation in leaf type, usually having cuneate or truncate basal leaves.

The stems of *R. micranthus* are consistently pilose, those of *R. Harveyi* are pubescent in a form of sporadic occurrence, and those of *R. abortivus* are pubescent in a geographic variety. In *R. abortivus*, pubescence of petioles is variable even on the same plant. Pubescence of receptacles is a specific character in this group.

Suggestions

In the intermediate region occupied by both typical *R. abortivus* and var. *acrolasius* it is yet to be determined whether or not there is any correlation of ecological conditions and the proportion of each variety within a colony.

In the Black Hills of South Dakota, only var. *acrolasius* has been found, but the typical form is listed by Fernald as reaching southern Saskatchewan. This would indicate that the plant reached the Black Hills from the north or west, not from the southeast by way of the Missouri River and its tributaries as many plants are thought to have come.² In this case, the migration of the southern, glabrous plant into southern Canada was probably later. Mass collections throughout the Dakotas and adjacent states and provinces should throw additional light on the always intriguing problem of the origins of the floras in the Black Hills.

The validity of the separation of the more northern *R. micranthus* var. *delitescens* with basal leaves having greater tendency to being cordate than in the more southern typical *R. micranthus*, should be tested by means of mass collections.

² See Hayward, Bot. Gaz. 85:379. 1928.

Post-Mount Mazama Forest Succession on the East Slope of the Central Cascades of Oregon¹

Henry P. Hansen

Introduction

The eruption of the prehistoric volcano, Mount Mazama, that formed the caldera holding Crater Lake in the Cascade Range of southern Oregon, occurred between 5,000 and 10,000 years ago (Williams, 1941). This volcanic activity resulted in the deposition of a pumice mantle, that extends with diminishing thickness to the east and north of Crater Lake. The depth of the pumice varies from more than 10 feet in the vicinity of Crater Lake to several inches about 100 miles to the north. The pumice lies chiefly on the east slope of the Cascade Range. This cataclysmic event and the enormous amount of pumice and other types of ejecta deposited in this region must have had a profound effect upon the forests that existed at the time of the eruption. Forests in the immediate vicinity of Mount Mazama were probably instantly destroyed by the fragmental ejecta and the incandescent gases that descended the slopes of the mountain. Forests growing beyond the influence of these factors were probably less precipitately destroyed by the pumice mantle and the sudden change in the edaphic conditions. In areas still farther removed from Mount Mazama the forests were not killed, but the change in the edaphic conditions must have inhibited the growth of seedlings of those species that composed the existent forests. Eventually, as the trees of these forests died of old age or were destroyed by wind, fire, or disease, they were replaced by other species less exacting as to soil requirements. Such species were further benefited by lack of competition.

Location and Characteristics of the Bogs

The peat deposit of this study located nearest to Crater Lake lies in Munson Valley on the south slope of the mountain. Munson Creek rises near the south rim of the caldera and flows directly south to empty into Annie Creek, about 4 miles beyond the rim of Crater Lake. The bog is located in section 17 of T. 31 S., R. 6 E., and at an elevation of about 6200 feet. It comprises several acres and is covered chiefly with sedge (*Carex* spp.) and willow. Lodgepole pine (*Pinus contorta*) is the pioneer forest tree invader followed by alpine fir (*Abies lasiocarpa*). The depth of the pollen-bearing sediments in the area of sampling is 2 meters, which was the deepest point located. The lowest level is composed of a fine, gray, silty sediment, which upon examination under the microscope was found to consist of almost pure volcanic glass. The presence of pollen

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at this level suggests that the glass was transported into ponded water rather than having been deposited *in situ* during the eruption. The glass grades upward into fibrous peat. Pure fibrous peat is present from 1.2 meters to the surface. It is impossible to estimate the amount of time that elapsed between the eruption of Mount Mazama and the initiation of the pollen-bearing sedimentation. Munson Valley was eroded in Mount Mazama volcanic material. The depth of the peat, however, suggests that from 5,000 to 7,000 years were required for its deposition. The average rate of sedimentation in post-Pleistocene peat bogs in the Pacific Northwest has been about one foot per thousand years. In a bog located near Bend, Oregon, two layers of pumice occur at 2 and 4.5 meters respectively in a 7-meter profile (Hansen, 1942b). It seems probable that the upper stratum owes its origin to the eruption of Mount Mazama, because this bog lies in a zone where the pumice mantle is several inches thick. The depth of the peat above the upper layer of pumice is about the same as the entire Munson Valley profile.

Another peat profile was obtained from Big Marsh, which is located 30 miles north of Crater Lake. This bog has developed on the floodplain of Big Marsh Creek, and is about 3 miles long and 1 mile wide. The surface is covered largely with sedge (*Carex* spp.) and willows. In addition to the sluggish stream that flows through the bog, there are several sloughs supporting various stages of hydrarch plant succession. The sloughs suggest a meandering stream, which may have removed some of the peat in certain areas. There is no topographic map of the region, but the bog lies at an elevation between 4,000 and 5,000 feet. Peat samples were obtained in section 18 of T. 25 S., R. 7 E. The depth of the bog in the area of sampling is 1.8 meters. The peat rests directly upon coarse pumice which the peat borer would not penetrate. The thickness of the pumice mantle in this area varies from 5 to 10 feet.

Peat samples were obtained from a third bog located about 50 miles north of Crater Lake and about 22 miles northwest of Big Marsh. It is located in section 28 of T. 22 S., R. 5 E. at an elevation of 2900 feet, about 10 miles west of the Cascade divide near the Willamette Pass highway. The peat has accumulated at the junction of the South Fork of Salt Creek and a small tributary. The bog comprises an area of about one and one-half acres, and is nearing the climax stage of plant succession. Trees invading the bog in order are Engelmann spruce (*Picea engelmanni*), mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), and alpine fir. On the margin grow mountain alder (*Alnus tenuifolia*) and willow. Lesser vegetation present consists of bog laurel (*Kalmia polifolia*), blueberry (*Vaccinium uliginosum*), shooting star (*Dodecatheon jeffreyi*), star-flower (*Trientalis latifolia*), twin-flower (*Linnaea borealis*), bunchberry (*Cornus canadensis*), mitrewort (*Mitella ovalis*), paint-brush (*Castilleja* sp.), marsh marigold (*Caltha leptosepala*), skunk cabbage (*Lysichitum americanum*), and a few species of sedge (*Carex* spp.). The bog lies in an area where the Mount Mazama pumice mantle is several inches thick. The depth of the peat at the deepest point that could be found is 2.75 meters. The peat is underlain with coarse sand rather than

pumice. A stratum of pumice is present at 2.5 meters, which suggests that the eruption of Mount Mazama occurred just after the beginning of sedimentation. Fibrous peat is present from 2.25 meters to the surface.

Peat samples were also obtained from a fourth bog located on the margin of Mud Lake, about 70 miles north of Crater Lake and 20 miles west of Bend. Mud Lake is about one and one-half miles long and shaped like a dumb-bell. Both ends of the lake support various stages of hydrarch plant succession. Borings were made near the south end where there are several well-defined zones of hydrophytic vegetation. A floating sere of yellow pondlily (*Nymphaeodanthus polysepala*), is followed shoreward by a zone of pondlily and bulrush (*Scirpus validus*), which in turn is succeeded by a zone composed of bulrush, sedge (*Carex* sp.), and buckbean (*Menyanthes trifoliata*). The last grades into a more mesophytic zone consisting chiefly of sedge, purple marshlocks (*Potentilla palustris*), and bog laurel. A few specimens of lodgepole pine have gained a foothold in the mesophytic areas. Samples were obtained in section 4 of T. 19 S., R. 8 E. where the profile is 1.8 meters deep. The peat is underlain with coarse pumice which was impenetrable with a Hiller peat borer. Mud Lake lies at an altitude of 5,000 feet and in an area where the pumice mantle is between one foot and six inches thick. Bachelor Butte, an extinct volcanic cone, reaching an elevation of more than 9,000 feet, is situated about 4 miles to the east.

In the preparation of the peat for microscopic analysis, the potassium hydrate method was used. From 100 to 200 pollen grains were identified from each level. Pollen of species not considered as indicators of forest succession was also identified as to genus and listed in the tables. The identification of the winged conifer pollen was based upon the size-range method which has been described in previous papers (Hansen, 1941a, 1941b, 1941c). As stated in these papers, it is not possible to separate all of the species of *Pinus* and *Abies*. In this study the most significant inseparable species are western white pine and white bark pine (*Pinus albicaulis*). Pollen of these species is listed under white bark pine. In the Munson Valley bog, most of the pollen thus listed is probably of this species. In the Willamette Pass bog, however, it seems probable that most of the pollen is that of western white pine because of the moister climate and lower elevation of adjacent areas. In the Big Marsh and Mud Lake bogs it is not possible to say which species of pollen is predominant. Other indistinguishable species of less importance, because of low proportions of their pollen present, are white fir (*Abies concolor*) and noble fir (*A. nobilis*), and lowland white fir (*A. grandis*) and silver fir (*A. amabilis*). The first two are listed as white fir and the last two are recorded as lowland white fir. Sugar pine (*Pinus lambertiana*) and yellow pine (*P. ponderosa*) are inseparable to some extent because a small percentage of the former's pollen is within the size-range of that of yellow pine. The feasibility of the size-range is substantiated by the consistencies of pollen profiles from the same bog or bogs located within the same forest climax. In four sediment profiles from Lower Klamath Lake of Oregon and California, a remarkable similarity is present for the general trends of lodgepole, yellow, and white pine pollen spectra

(Hansen, 1942a). In other peat deposits the relative pollen proportions of the several species represented at the surface seem to correlate fairly well with their relative abundance in adjacent areas.

Forests in Adjacent Areas

The four peat deposits of this study lie near the crest of the Cascade Range. The Willamette Pass bog is located a few miles to the west of the divide, whereas the other three are situated just east of the summit. The Munson Valley bog lies practically astride the border of the Hudsonian and Canadian life zones, and the others are located within the Canadian zone (Bailey, 1936). All peat deposits are in proximity to both the Hudsonian and Arctic-alpine life zones, and pollen from the forests of these zones is recorded in the peat profiles. The timbered Arid Transition lies about 10 miles south of the Munson Valley bog, 25 miles east of Big Marsh, 5 miles east of Mud Lake, and 25 miles east of the Willamette Pass bog. The boundary of the Humid Transition is located only 10 miles west of the last bog, and the same zone is about 10 miles west of Crater Lake. The Canadian zone is the most extensive in proximity to the peat deposits, and the timbered Arid Transition is next in extent of area. The borders of life zones, forest climax regions, and climatic provinces are irregular in mountainous areas, extending upward or downward beyond the general limits where the conditions are favorable.

The most abundant species of conifers in the Canadian zone are western white pine, western hemlock (*Tsuga heterophylla*), Engelmann spruce, noble, silver, lowland white, and white fir, and sugar and white pine. Lodgepole pine is confined largely to the pumice-covered areas and is more abundant east of the Cascade divide than it is to the west. On the west slope of the Cascades, Douglas fir (*Pseudotsuga taxifolia*), western hemlock, and silver and lowland white fir become more abundant. The timbered Arid Transition, from the latitude of Crater Lake to 100 miles north, is forested about equally with western yellow and lodgepole pine. It is this area that has the greatest thickness of pumice, which extends east and north of Crater Lake in diminishing depth. Lodgepole probably persists here as a subclimax, because the climate of this area is such as normally to support forests of the Canadian zone in its upper part, and yellow pine forests in the areas at lower elevations. Forest type maps (1936) show that yellow pine forms a continuous zone to the east of the lodgepole pine forests and as far north as Bend. Still farther north, yellow pine forms a solid, continuous, but narrowing belt, almost to the Columbia River. The lodgepole pine zone gradually tapers to nothing northward, and is practically absent for the last 100 miles to the Columbia River. This may be due to both the absence of pumice and a difference in climate. The yellow pine forests here lie closer to the Cascade divide.

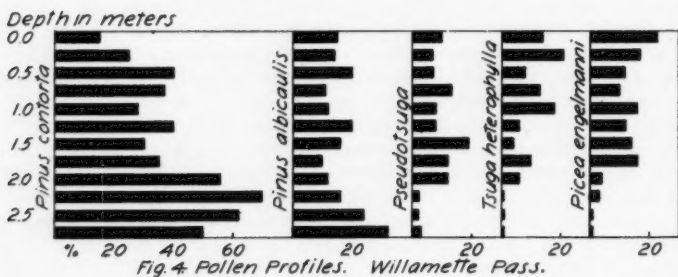
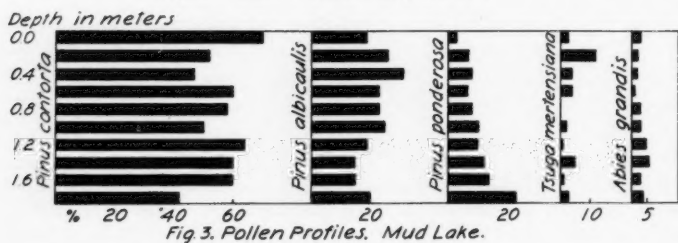
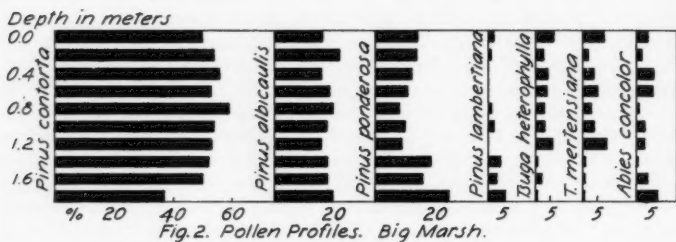
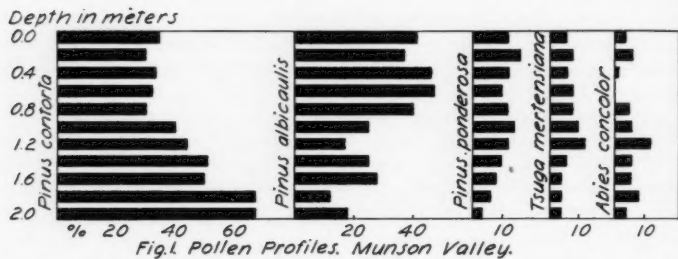
The Hudsonian, immediately above the Canadian zone, is forested with alpine types including mountain hemlock, white bark pine, alpine fir, and Alaska cedar (*Chamaecyparis nootkatensis*). Lodgepole also is abundantly

present in this zone. In general it can be said that lodgepole pine is the chief dominant over almost one-half of the timbered belt on the east slope of the Cascade Range for a distance of 100 miles north of Crater Lake. It is also present in greater or lesser proportions in forests of adjacent areas. The altitude of the site of the Munson Valley bog is the highest and the forests of the Hudsonian zone are best represented in this peat profile. A detailed study of the life zones and flora of Crater Lake National Park has been made by Wynd (1941). His observations show that the Hudsonian forests consist largely of mountain hemlock and white bark pine, and those of the Canadian zone are composed chiefly of lodgepole pine.

The bogs of this study are located within a climatic province designated as having a humid, microthermal climate, with adequate precipitation at all seasons (Thorntwaite, 1931). The mean annual precipitation, however, varies considerably in the four areas. The greatest occurs at Crater Lake with about 53 inches (Weath. Bur., U.S.D.A., 1936). At Crescent, 12 miles northeast of Big Marsh but at a lower elevation, it is 19.25 inches. At Sisters, 25 miles northeast of Mud Lake, the mean annual precipitation is 16.65. At Crater Lake, 16 per cent occurs from May to September inclusive, and at Crescent and Sisters 24 and 21 per cent respectively occurs during the same period. The growing season is thus relatively dry, and the porosity of the pumice probably permits rapid drainage, thereby decreasing the benefits of rain during the growing season. It should be noted that the precipitation in the vicinity of Mud Lake and Big Marsh is greater than at Sisters and Crescent respectively, because of their higher elevation. The prevailing wind direction during the period of anthesis is westerly, which is reflected by the relatively low proportions of yellow pine pollen in the peat profiles. This is probably due to the existence of the yellow pine belt to the leeward of the bogs.

Post-Mount Mazama Forest Succession

The location of the bogs in relation to the climate and the depth of the pumice mantle is well reflected by their pollen profiles. Those of Big Marsh and Mud Lake are similar in their general trends. This is to be expected because of the location of the peat deposits in similar floristic and climatic provinces. The pollen profiles of the Munson Valley bog differs from the others because of its higher elevation and different climate. The Willamette Pass bog also records different forest succession because of its location west of the Cascade divide in an area of moister climate and where the pumice mantle is not as thick. On the slopes below Crater Lake lodgepole and white bark pine have been predominant as recorded by their pollen spectra (Fig. 1). These species contributed 67 and 18 per cent respectively of the pollen in the lowest level. Lodgepole pine shows a general decline from the lowest level to the surface where it is recorded to 35 per cent, whereas white bark pine marks a general increase upward to be recorded to 41 per cent at the surface. The lowest percentage of lodgepole pine pollen in the profile is 30, whereas the highest for white bark pine is 47 at 0.6 meter. Other conifers appreciably recorded in order are yellow pine, mountain hemlock, and white fir (Fig. 1).



In the Big Marsh peat profile, lodgepole pine is recorded as having been predominant by a wide margin during all of post-Mount Mazama time (Fig. 2). It contributed 37 per cent of the pollen present in the lowest stratum, shows a gradual increment to 59 per cent at 0.8 meter, and then slightly declines to the surface where it is recorded to 50 per cent. White bark and white pine, whose pollen is inseparable, is next in abundance to lodgepole. These species apparently remained rather constant in their abundance during

TABLE 1.—Percentages of Fossil Pollen. Munson Valley Bog.

Depth in meters	2.0	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0.0
<i>Pinus contorta</i>	67	67	50	51	44	40	30	32	33	30	35
<i>P. albicaulis</i>	18	12	28	25	17	25	40	47	46	37	41
<i>P. ponderosa</i>	3	6	8	10	12	14	12	10	12	16	12
<i>Tsuga mertensiana</i>	4	4	4	6	12	10	8	8	6	8	6
<i>Abies grandis</i>	2	2	..	1	4	4	1	..	1	1
<i>A. concolor</i>	4	8	6	6	12	6	5	..	1	6	4
<i>A. lasiocarpa</i>	4	1	2	2	2	..	1	2	1	2	..
<i>Picea engelmanni</i>	1	1	..	1
<i>Pinus</i> spp.*	8	14	23	10	15	11	10	13	19	11	17
<i>Abies</i> spp.*	4	1	4	3	4	3	2	2	2	..	1
Gramineae*	1	1	1
Compositae*	4	1	1	1	4	1
Chenopodiaceae*	1
<i>Alnus</i> *	1	3	1	1
<i>Acer</i> *	1	..	1	1	1	..	1
<i>Salix</i> *	3	3	1	2	1
Cyperaceae*	2	8	10	12	13	13	25	34	59	22	23

* Number of pollen grains; not computed in the percentages.

TABLE 2.—Percentages of Fossil Pollen. Big Marsh Bog.

Depth in meters	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0.0
<i>Pinus contorta</i>	37	50	52	53	54	59	53	56	54	50
<i>P. albicaulis</i>	20	18	18	16	18	20	19	16	22	16
<i>P. ponderosa</i>	25	16	19	9	10	8	11	10	12	12
<i>P. lambertiana</i>	6	3	4	..	2	1	1	2
<i>Pseudotsuga taxifolia</i>	1	1	1	1	3	1	1	3	3	2
<i>Tsuga heterophylla</i>	1	2	1	6	3	4	4	4	3	6
<i>T. mertensiana</i>	1	1	1	8	4	3	5	4	2	7
<i>Abies grandis</i>	1	1	..	1	1
<i>A. concolor</i>	7	4	1	3	3	1	6	6	2	4
<i>A. lasiocarpa</i>	1	1	2	2	1	1
<i>Picea engelmanni</i>	1	2	1	4	1	..	1	..
<i>Larix occidentalis</i>	1	..	2
<i>Pinus</i> spp.*	18	11	14	11	11	10	13	11	13	15
<i>Abies</i> spp.*	2	4	1	1	6	1	3	2
Compositae*	2	1	2	..	1	1	..	1	1	6
<i>Alnus</i> *	1	1	..	1	1
<i>Acer</i> *	3	1
<i>Salix</i> *	1	..	2	18
Cyperaceae*	16	17	32	37	44	37	77	72	70	85
<i>Nymphozanthus</i> *	1	1

* Number of pollen grains; not computed in the percentages.

the time represented by the peat profile. They are represented by 20 per cent of the pollen at the bottom, and fluctuate between 16 and 22 per cent throughout the rest of the spectrum. Yellow pine is third in importance. It is recorded to 25 per cent at the lowest level, declines to 8 per cent at 0.8 meters, and then increases slightly to 12 per cent at the top. Mountain and western hemlock and white fir are also recorded by appreciable proportions. The first two species probably existed in moister areas to the west, windward to the site of the sediments.

TABLE 3.—Percentages of Fossil Pollen. Mud Lake Bog.

Depth in meters	1.8	1.6	1.4	1.2	1.0	0.8	0.6	0.4	0.2	0.0
<i>Pinus contorta</i>	42	60	60	64	59	58	63	47	52	70
<i>P. albicaulis</i>	20	15	15	19	25	23	23	31	26	19
<i>P. ponderosa</i>	23	14	12	10	10	8	7	8	7	3
<i>P. lambertiana</i>	2	1	2	2
<i>Pseudotsuga taxifolia</i>	1	3	1	..	2	2	1	..	1	..
<i>Tsuga heterophylla</i>	2	2	1	..	2	1	1	3	..	1
<i>T. mertensiana</i>	3	1	5	1	2	..	4	4	12	3
<i>Abies grandis</i>	4	3	6	5	3	3	1	2	2	3
<i>A. concolor</i>	2	1	2	1	1
<i>A. lasiocarpa</i>	1	2	..	1	3	..	1
<i>Picea engelmanni</i>	1	1	1	1	1	1
<i>Pinus</i> spp.*	15	10	16	11	15	10	19	12	11	16
<i>Abies</i> spp.*	2	1	1	2	3	1	1	1	3	2
Compositae*	1	..	1
<i>Alnus</i> *	1	..	2	..	1	..	3	..	1	..
<i>Acer</i> *	1	1	1
Cyperaceae*	34	46	14	14	23	40	45	30	60	16
<i>Nymphozanthus</i> *	4	1	2	1	1

* Number of pollen grains; not computed in the percentages.

TABLE 4.—Percentages of Fossil Pollen. Willamette Pass Bog.

Depth in meters	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.5	0.25	0.0
<i>Pinus contorta</i>	50	62	70	56	35	30	40	28	37	40	25	15
<i>P. albicaulis</i>	32	24	16	12	10	16	20	12	11	20	14	15
<i>P. ponderosa</i>	4	4	1	..	1	1	1	1	1	4	2	2
<i>P. lambertiana</i>	1	3	..	3	1	1	1	2	..
<i>Pseudotsuga taxifolia</i>	3	2	2	12	19	8	8	13	7	7	10	..
<i>Tsuga heterophylla</i>	1	1	1	6	10	4	6	18	13	8	21	14
<i>T. mertensiana</i>	6	1	..	6	2	1	1	..	1	3
<i>Abies grandis</i>	2	1	..	5	2	8	10	8	10	8	2
<i>A. concolor</i>	3	2	3	4	6	13	4	6	2	3	2	6
<i>A. lasiocarpa</i>	4	3	2	3
<i>Picea engelmanni</i>	1	1	3	4	16	14	12	16	10	12	17	23
<i>Pinus</i> spp.*	17	13	17	19	10	7	8	12	8	10	15	15
<i>Abies</i> spp.*	2	1	8	2	9	3	5	3	1	3	2	4
Gramineae*	1	2	1
Compositae*	1	2	2	1	..
<i>Alnus</i> *	1	1	3	12	8	13	5	7	8	6	2
<i>Acer</i> *	1	1	2	..	1	3	2	2	4	1	3	5
<i>Salix</i> *	1	2	1	..	2	3	1	2	5	11
Cyperaceae*	1	10	5	7	4	3	2	1	4	3	5	1

* Number of pollen grains; not computed in the percentages.

The trends of the pollen profiles recorded in Mud Lake bog are similar to those of Big Marsh. Lodgepole has likewise been the predominant species in its vicinity (Fig. 3). It contributed 42 per cent of the pollen at the bottom, and with several sharp fluctuations it increases to 70 per cent at the surface. White bark and white pine are slightly better represented in Mud Lake bog than in Big Marsh, perhaps because of the former's proximity to the Hudsonian zone along the crest of the Cascade Range. These species are represented by 20 per cent at the bottom, attain 31 per cent at 0.6 meters, and then decline to 19 per cent at the surface. Yellow pine is recorded to 23 per cent at the lowest horizon, and then gradually declines to only 3 per cent at the top. Mud Lake is farther removed from yellow pine forests than Big Marsh. The former lies entirely within lodgepole pine forests, whereas the latter is situated adjacent to yellow pine types. Other conifers most abundantly and consistently recorded are mountain hemlock and lowland white fir (Table 3).

The moister climate and thinner pumice-mantle in the vicinity of the Willamette Pass bog is reflected by the forest succession as recorded in the peat profile. As previously stated, sedimentation of the peat was initiated just prior to the eruption of Mount Mazama. Lodgepole pine is recorded to 50 per cent at the lowest level and then increases sharply to 70 per cent at 2.25 meters. The eruption of Mount Mazama apparently occurred some time during the deposition of the lower one-half meter of peat. The pronounced predominance of lodgepole pine, however, was short-lived, as it shows a sharp decline to 30 per cent at 1.5 meters (Fig. 4). It then fluctuates between 28 and 40 per cent to 0.5 meters, and makes a final decline to 15 per cent at the surface. The last proportion is the lowest for lodgepole in any of the profiles. The general decline of this species from 2.25 meters to the surface is suggestive of rapid modification of the pumiceous soil favorable for the development of other species. The moister climate probably augmented the rate of soil modification. White bark and white pine decline from 32 per cent at the bottom to 10 per cent at 1.75 meters, from which horizon they vary from 11 to 20 per cent to the uppermost stratum (Fig. 4). The general trend for these species seems to be similar in the four peat profiles. Other conifers represented by their pollen in appreciable proportions are Douglas fir, Engelmann spruce, and western hemlock. These species thrive better under moister conditions than lodgepole pine, are more tolerant of shade, and also are more exacting as to edaphic conditions. Western hemlock is particularly so, and grows best where there is considerable humus in the soil. These species show a general increase from 2.25 meters to the surface (Fig. 4). Douglas fir, spruce, and hemlock are recorded to 1, 3, and 2 per cent respectively at this level, and are represented by 10, 23, and 14 per cent at the surface. Yellow pine is sparsely recorded throughout the profile with a maximum of only 4 per cent. Other conifers recorded in low proportions are sugar pine, mountain hemlock, and lowland white, white, and alpine fir (Table 4).

There seems to be little or no evidence for climatic trends in the pollen profiles during the period of time represented by the peat profiles. The existence of the pumice has apparently been unfavorable for the maintenance of

yellow pine as the climatic climax over most of this region. Lodgepole pine, which is a subclimax species that thrives in edaphically disturbed areas, was able to gain predominance due to lack of competition. This species was the chief postglacial pioneer invader of deglaciated regions in other parts of the Pacific Northwest (Hansen, 1938, 1939a, 1939b, 1940a, 1940b, 1041a). It was gradually replaced entirely or partially by other species as the rigorous conditions left in the wake of the glacier were ameliorated. In the Puget Lowland of western Washington it was replaced by Douglas fir, in eastern and north central Washington by yellow pine, and in northern Idaho by western white pine. In the vicinity of Mud Lake, it is probable that lodgepole existed as the predominant species before the eruption of Mount Mazama. This is indicated by pollen profiles of a peat deposit at Tumalo Lake, 13 miles to the northeast (Hansen, 1942c). Lodgepole pine gained predominance soon after a volcanic eruption as denoted by a stratum of pumice at 4.5 meters, which it was able to maintain until and after a second eruption recorded at 2 meters. This upper pumice stratum presumably owes its origin to Mount Mazama, and the recorded forest succession above it is similar to that of the entire profiles of both Big Marsh and Mud Lake bogs. The source and extent of the lower pumice layer is unknown, but it may be localized in the vicinity of the Three Sisters.

There are several lines of evidence suggesting that the eruption of Mount Mazama occurred during or soon after a recorded dry period between 4,000 and 7500 years ago. Pollen profiles from Lower Klamath Lake indicate a period of desiccation about this time as based upon the forest succession and the depth of sediments (Hansen, 1942a). This is further evidenced by an artifact horizon underlying 6 to 8 feet of peat (Cressman, 1940). Apparently the lake dried up and early man built his camp sites upon the lake bed. A moister climate resulted in re-inundation of the lake bed and the subsequent deposition of 6 feet of peat. Although Lower Klamath Lake is located beyond the range of air-borne pumice from Mount Mazama, the highest proportions of lodgepole pine pollen in three out of four profiles are attained just after the yellow pine maximum and above the artifact horizon in each of the profiles. This suggests that the eruption of Mount Mazama occurred during or soon after the dry period denoted by the maximum attained by yellow pine. The thickness of the peat above the artifact horizon is also correlative with the depth of the peat profiles of this study. Peat profiles in the lower Willamette Valley have a pumice stratum immediately above the maximum of white oak (*Quercus garryana*), which is sufficiently high to indicate a period of desiccation in this area (Hansen, 1942b). The source of the pumice is not known, but if it is from Mount Mazama it shows significant correlation with the interpretations of the Lower Klamath Lake profiles. The existence of a dry period about this time is also suggested by the salinity of certain lakes in the Great Basin (Antevs, 1938), and the oscillations of montane glaciers in some of the western mountains (Matthes, 1939).

Summary

Forest succession on the east slope of the central Cascades in Oregon since the eruption of Mount Mazama has been influenced largely by the thick pumice mantle that extends north and east of Crater Lake. The pollen profiles of four peat bogs lying directly upon Mount Mazama pumice show trends of forest succession that reflect each bog's location with respect to climate and the thickness of the pumice in adjacent areas.

In all profiles lodgepole pine was predominant when deposition of the pollen-bearing sediments began. In the Mud Lake and Big Marsh bogs, lodgepole is recorded as having been predominant throughout the entire period represented by the peat profiles. In the Munson Valley bog, the high elevation and cooler climate is reflected by an increase in white bark pine to supersede lodgepole pine about half-way up in the profile. In the Willamette Pass bog, lodgepole pine decreases from the time of the pumice eruption to the present. Douglas fir, western hemlock, and Engelmann spruce show a general increase from bottom to top. Their greater abundance here may have been a result of more rapid modification of the thinner pumice mantle in this area.

There is little evidence for climatic trends. The Munson Valley and Willamette Pass pollen profiles suggest a slight increase in moisture, and possibly some cooling to a maximum during post-Mount Mazama time. The depth of the peat profiles, and the rate of peat formation in the Pacific Northwest suggest that the eruption of Mount Mazama occurred between 5,000 and 7500 years ago.

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Book Reviews

THE EVOLUTION OF GENETIC SYSTEMS. By C. D. Darlington. Cambridge: at the University Press; New York: The Macmillan Company, 1939. x + 149 pp. Price \$2.75.

This is a small book on a large subject. The 133 pages of exposition take one from the fundamentals of cytogenetics up through the experimental and observational data which have resulted in Darlington's formulating his theories concerning evolution. To one who is aware of the subject this, if the author has done it satisfactorily, is an accomplishment of the first magnitude.

In the first twenty chapters Darlington describes, in addition to the introductory facts of genetics and cytology, the genetical and cytological types, their control, their variation, their inter-relations, their evolutionary significance, etc. This portion of the book serves as a preliminary to the last chapter.

In this chapter, "The Evolution of Heredity," Darlington summarizes his ideas concerning the development of these systems. He says that the systems can be put into "three important levels of organisation." These levels have evolved in a series beginning with the lowest in which there is no genic differentiation. These undifferentiated genes became arranged linearly and a method—mitosis—appeared to preserve this arrangement. This marks the attainment of the second level—it "has a differentiation of genes but no sexual reproduction." Then the appearance of meiosis, a modification of mitosis, resulted in sexual reproduction, and, subsequently, with a delay between successive periods of meiotic activity during which mitotic divisions and cellular differentiations occur, there emerged the third level, viz., sexual reproduction with an alternation of haploid and diploid phases. In addition to these levels of organization of genetic systems, he recognizes the division of the system into "levels of integration" such as the gene, chromosome, etc. These are operated upon by the environment and, as variations at these levels occur, the environment selects. Selection is not directed against the biological unit alone; it "acts upon the genetic system at every level, gene or chromosome, cell and individual, and in every state and process, haploid and diploid, mitotic and meiotic, embryonic and adult." He concludes with the statement that the evolutionary potentialities of a genetic system are dependent upon the qualities of its various levels of integration from its "cytoplasmic molecules" up, and "... at these levels, both severally and relatedly, natural selection controls the destiny of the system."

The above paragraph, although certainly not an exhaustive description of Darlington's ideas, is sufficient to indicate the scope of them and their direction. It is plain that there are some wide generalizations that cannot be elegantly defended. Perhaps, however, such statements are to be expected to some extent in writing of this sort. But it is difficult to overlook the dogmatic tone in which many very questionable statements are presented. An example of this is the sentence found on page 123: "The plasmagene is a relic of the naked gene of pre-chromosomian times, a relic which is preserved..." etc. That, of course, is pure fancy on Darlington's part, and it is but one of the instances in which he represents as fact statements which are highly theoretical.

Darlington in the preface claims that the work is an "elementary exposition." That should not be interpreted as an indication that the uninitiated can read the book with the hope of evaluating correctly the ideas developed. The brevity of some of the early basic chapters together with the dogmatism referred to above precludes this.

—E. LAWRENCE POWERS, JR.

FLOWERS AND FLOWERING PLANTS. By Raymond J. Pool. McGraw-Hill Book Company, New York, 1941. Second Edition, xxiii + 428 pp., frontispiece, 211 figs. \$3.50.

Like the first edition the present one is based on Bessey's system and as such is the only modern exposition of it. The most conspicuous change is the appearance of an entirely new chapter dealing with "the more prominent vegetative features that are helpful in taxonomic work." Minor changes include a simplified chart (fig. 69) in place of its more "puzzling" forerunner, a new diagram of the suggested relationships of the major orders as rearranged by Clements (p. 352), the rearrangement of certain chapters, the addition of "valuable American works that have been published since 1929," and a brief glossary.

That the vegetative characters are given recognition is certainly commendable in view of their importance and of the increasing interest they demand from a morphological point of view. Unfortunately, no use is made of the recent significant work in wood anatomy and its bearing on the classification of difficult orders and families. Another serious omission is the almost complete neglect of the gametophytic generation, e.g., the absence of suitable illustrations of embryosacs and embryosac types, etc. Perhaps this generation is the sole concern of the morphologist though considerable taxonomic value may be attached to these characters if used in conjunction with others. Regardless of the viewpoints expressed, important and informative works such as E. R. Saunders' "Floral Morphology," Agnes Arber's "The Gramineae," the second volume of Hutchinson's "The Families of Flowering Plants," Albert Lemée's "Dictionnaire descriptif et synonymique des genres de plantes phanérogames," American floras like Deam's "Flora of Indiana," Marie Victorin's "Flore Laurentienne" could profitably have been added to the bibliography. Although one might argue regarding the place of the "Index Kewensis" etc. in an elementary text of this sort, students should become acquainted with such fundamental reference works rather than with some of the lesser ones listed. In the transfer of chapters it might have been expedient to drop the last sentence on p. 353, since neither the chapter immediately following nor the last one is concerned with the promised "principles of classification." Perhaps two pages or so might have been used for the benefit of the student to present a list or, possibly, a short discussion of the important botanical gardens and herbaria in the United States. A few words regarding modern and, for the most part, American herbarium methods would bring that chapter up to date. Finally, would it be too unorthodox to suggest that future textbooks of systematic botany should include chapters devoted to the exposition of the principles of cytogenetics and their application in taxonomic and phylogenetic work when we possess modern floras listing the known chromosome numbers of numerous species?

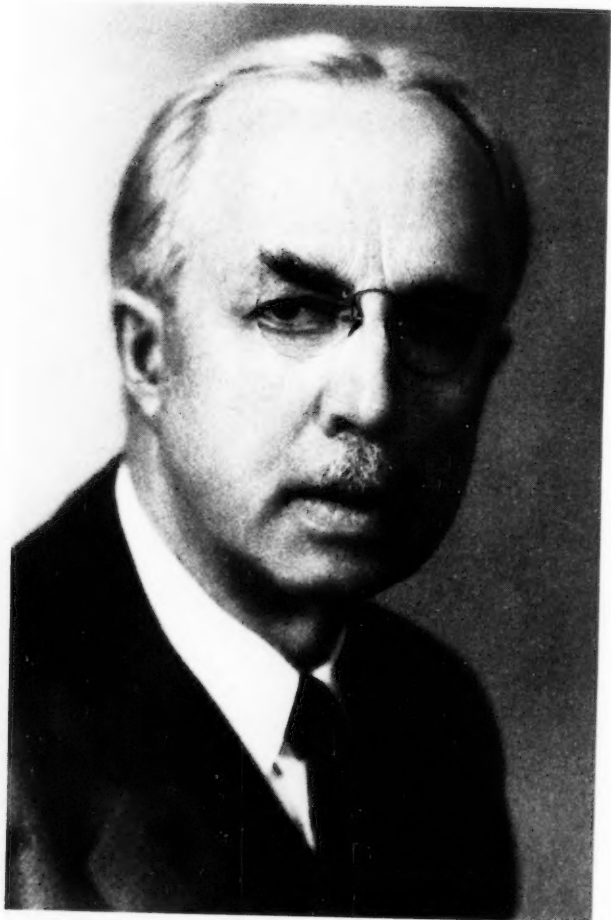
Opinions may differ regarding the pedagogic value of these suggestions but modern taxonomy is increasingly dependent upon the findings of other biological sciences in its effort to arrive at a "natural" classification. Thus the "new systematics" differs readily from the "old" or as Julian S. Huxley puts it, "To hope for the new systematics is to imply no disrespect for the old."—THEO. JUST.

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MARCUS WARD LYON, JR.

Marcus Ward Lyon, Jr.

1875 - 1942

ON MAY 19, 1942, Dr. Marcus Ward Lyon, Jr., zoologist, bacteriologist and pathologist, passed away in his home in South Bend, Indiana, and a few days later was buried in Arlington National Cemetery. His death terminated an unusually full and highly productive life.

Marcus Ward Lyon, Jr. was born February 5, 1875, in Rock Island Arsenal, Illinois, the oldest son of Captain Marcus Ward Lyon, U.S. Army, and Lydia Anna Lyon, and spent his early life at army posts in various parts of the country. After graduating from Rock Island High School in 1893, he entered Brown University the same year and received his Ph.B. in 1897. He spent the following year (1897-1898) at North Carolina Medical College as instructor in bacteriology. In 1898 he moved to Washington, D. C. and began the two distinct careers so characteristic of his whole life. He was appointed Aid, and later Assistant Curator in the Division of Mammals, U.S. National Museum, and at the same time embarked on his graduate studies at George Washington University, where he secured his M.S. degree in 1900, his M.D. in 1902, and his Ph.D in 1913. He maintained his connections with the U.S. National Museum until 1912, while teaching physiology (1903-1904, 1907-1909) and bacteriology (1909-1915) in the Medical School of Howard University and later bacteriology and pathology (1915-1917) as well as veterinary zoology and parasitology (1917-1918) in the Medical School of George Washington University. During World War I he joined the U.S. Army and served as pathologist in Walter Reed General Hospital from 1917-1919, attaining the rank of Major in the Medical Reserve Corps, September 1919. In 1902 he married Martha Maria Brewer, of Lanham, Maryland (M.D., 1907, Howard University). In 1919 they accepted an invitation to join the

staff of the South Bend Clinic with which they were associated for many years. From 1931 on Dr. Martha Brewer Lyon maintained her own office as an ophthalmologist until her death (January 18, 1942), whereas Dr. Marcus Ward Lyon, Jr. remained on the staff as pathologist. He is survived by a daughter, Charlotte Lyon, Philadelphia, Pennsylvania, and two brothers, Henry S. Lyon, East Orange, New Jersey, and Col. James W. Lyon, U.S. Army, C.W.S., San Francisco, California.

In 1899 Marcus Ward Lyon, Jr. and Lieut. Wirt Robinson, U.S. Army, were sent by the U.S. National Museum to collect mammals in Venezuela. Subsequently Lyon was appointed Chief Special Agent for the U.S. National Museum and Smithsonian Institution for the Louisiana Purchase Exposition, St. Louis, 1904, and for the Lewis and Clark Exposition, Portland, Oregon, 1905. In 1911 he and his wife travelled in Europe visiting famous zoologists and seeing important museums. Alone or together they attended numerous scientific meetings until the very end.

Lyon's scientific interests date from his boyhood days when he collected insects and other animals in the vicinity of his father's posts, especially around Watertown Arsenal near Boston, Massachusetts. The remarkable breadth of these interests, once matured, is attested by his scientific writings, ranging from mammalogy to bacteriology, parasitology, pathology, and botany. Always observant in the field as well as in the laboratory, he readily found interesting material for scientific papers. In open discussions at scientific meetings he frequently offered his own information to supplement that just presented. His own collections are now incorporated in large American Museums, the zoological ones at the U.S. National Museum, his first herbarium containing plants from Oregon, etc., in the U.S. National Herbarium, Smithsonian Institution, and, after his death, a second herbarium of the plants of the Indiana Dunes and lower Michigan in the University Herbarium, University of Michigan. The last collection was made in his spare time and in the company of his wife and later of the Rev. J. A. Nieuwland, C.S.C., and the writer. Only physical incapacity finally kept him at home when the sun was out and the Red-wing Blackbirds could be seen in the early spring.

Although always deeply interested and actively occupied with medical science, his heart was in the study of the vertebrates, especially the mammals, both living and extinct. His contributions to mammalogy outnumber and outweigh the others and many are still the only competent treatments of the groups concerned, viz., *Classification of the Hares and their Allies* (1904), *Treeshrews: an Account of the Mammalian Family Tupaiidae* (his Ph.D. thesis, 1913), or serve as excellent sources for information on mammals in general, like his *Mammals of Indiana* (1936). Only this year has his *Catalogue of the Type-Specimens of Mammals in the United States National Museum, Including the Biological Survey Collection*, with Wilfred Hudson Osgood as co-author, been replaced by a new edition. Similar in character are his contributions to the as yet unfinished *Nomenclator animalium generum et subgenerum*, published by the Prussian Academy of Sciences in Berlin and edited by F. E. Schulze, to which he contributed the names of living and fossil mammals, exclusive of the Rodentia, and those of living and fossil amphibians. While studying the collections of mammals received at the U.S. National Museum from the Far East, he acquired not only great familiarity with this striking fauna but also became intimately acquainted with the geography of that region though he never was able to visit it [see especially his *Mammals of Banka, Mendanau, and Billiton Islands, between Sumatra and Borneo* (1906), *Mammals Collected in Western Borneo by Dr. W. L. Abbott* (1907), and *Mammals Collected by W. L. Abbott on Borneo and Some of the Small Adjacent Islands* (1911)].

His great love of the outdoors with its plant and animal life made him an ardent conservationist and spokesman for the cause of real protection of wild life as shown in his paper *Conservation from the Naturalist's Point of View* (1939). Here he expressed frankly what was wrong with many programs of conservation as proposed and carried out by incapable or irresponsible people. In his last paper he described the imaginary life of the Kankakee region before Man destroyed it. In the same way he gave up his cottage in the Indiana Dunes when the world at large discovered that refuge and changed it into a vacation-land. Wild life should not be regarded as a source of amusement through shooting, etc., but rather as an irreplaceable treasure.

Lyon's congenial nature, excellent sense of humor and great personal interest in the activities of his scientific colleagues induced him to join a number of scientific organizations or else his attainments made him eligible for honorary membership, i.e., Phi Beta Kappa and Sigma Xi. His active participation and scientific reputation brought him many honors; secretary of the Biological Society of Washington (1904, 1915-1919), president of the St. Joseph County Medical Society (1931), treasurer (1927-1932) and later president (1933) of the Indiana Academy of Science, president of the American Society of Mammalogists (1931-1933) and election to honorary membership a month before his death.

While in South Bend he found in the late Rev. J. A. Nieuwland, C.S.C., a stimulating and sincere friend with whom he collected many plants on numerous field trips and whose company he enjoyed immensely. Soon he became a regular contributor to the *American Midland Naturalist* and finally, upon the invitation of the writer, joined the editorial staff in 1935. In this capacity his wise counsel and great learning contributed very materially to the improvement of the journal. The *American Midland Naturalist* loses an able scientific adviser in the passing of Marcus Ward Lyon, Jr., whose almost paternal interest in the present editor will always remain one of his most fortunate experiences.—THEODOR JUST



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